# Community ecology and diversity of tropical anuran larvae

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zu Braunschweig
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**D i s s e r t a t i o n**


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## Publikationen

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## Tagungsbeiträge

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Strauß, A., 2009. Funktionale Diversität - funktionale Redundanz: Ein anderer Blick auf die Diversität von Kaulquappengemeinschaften. Ecology & Energetics meeting, Hamburg, Deutschland, 04. April 2009 (Vortrag).

Strauß, A., E. Reeve, R.-D. Randrianiaina, M. Vences & J. Glos, 2009. It's not just the number of species: tadpoles' functional diversity along environmental gradients. 6th International Tropical Zoology Symposium "Tropical Vertebrates in a Changing World", Bonn, Deutschland, 03.-08. Mai 2009 (Vortrag).

Strauß, A., R.-D. Randrianiaina, E. Reeve, M. Teschke, M. Vences & J. Glos, 2008. Tropical tadpole communities: distribution patterns and assembly rules. 101st Annual Meeting of the German Zoological Society, Jena, Deutschland, 19.-22. September 2008 (Vortrag).

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## Contents

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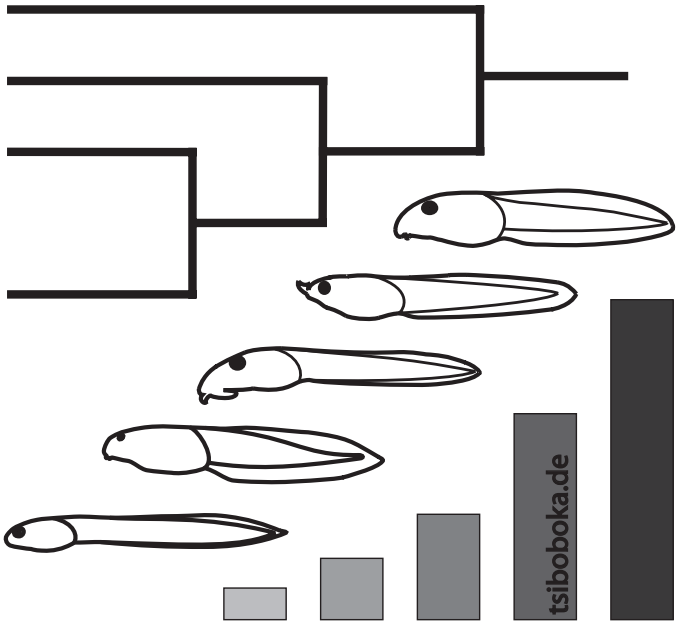

# General introduction

*The most impressive aspect of the living world is its diversity.*[1] Indeed, this diversity has attracted humans since millennia. Even earlier than 300 BCE, Aristotle already started first attempts to classify this diversity (Eldredge, 2002). Today we assume there might be about ten to twelve million species on earth, maybe more. Another important point beside this impressive richness, however, is that species almost never occur isolated from another – species coexist. Our understanding of rules of coexistence (and exclusion) is fundamental for the understanding of biodiversity. The latter in turn is a major key for conservation and human beings largely depend on biodiversity (Holt, 2001). Coexistence of species has therefore been an important topic in community ecology since a long time.

*Community ecology* – A species community is an assemblage of species populations that occur together in space and time (Begon et al., 1996). This is a rather general definition taking into account the existence of opposite views on communities: on the one hand, they were seen as strictly organised, structured, and integrated superorganisms that can repeatedly be found in space and time (Clements, 1916). On the other hand, communities were seen as a random collection of species occurring in the same time at the same place, only depending on species specific traits (Gleason, 1926). The truth, however, is somewhere in between (Underwood, 2008). There is certainly some interaction between species and with the environment in most communities, and it is the aim of community ecology to identify these interactions. In the 1950s, the earlier times of community ecology research represented by names like G. E. Hutchinson, N. Hairston., R. MacArthur and others, main attention was paid on competition as driving force in shaping communities (for an overview of references, see Kingsland, 1985). From the 70s on, further interactions such as predation were considered to be important, keeping population densities at low levels and therefore preventing competition (Connell, 1975, 1983). The same is true for abiotic environmental factors that were more and more considered to limit community growth and prevent them from reaching density levels with competition (Wiens, 1977, 1984). Consequently, the species community, its abiotic environment and their interactions form an integrated system. Already in 1935, A. G. Tansley coined the expression "ecosystem" for such systems (Salomon, 2008).

*Measuring diversity* – An important characteristic of a species community is its diversity, as it has paramount influence on properties of the whole ecosystem (Tilman, 1999). A wide range of

[1] Ernst Mayr; „This is Biology"

indices have been applied for quantifying diversity, the simplest of which is species richness (SR): the number of species in a community (Magurran, 2007).

However, the assumption that species are all comparable, distinct entities of similar ecological importance in the community and the ecosystem is oversimplifying. Therefore, in recent years more attention was paid on functional diversity (FD), which considers components that influence ecosystem function rather than taxonomic units (Tilman, 2001). FD provides more information on communities than SR (e.g., Tilman et al., 1997; Joshi et al., 2000) and was usually quantified via functional groups of species (Naeem & Li, 1997; Tilman, 2001; Tilman et al., 2001). An alternative and less arbitrary approach is the calculation of FD based on a range of traits of ecological importance rather than the focus on few key traits (Petchey et al., 2002; Petchey & Gaston, 2006).

A further measure of diversity receiving more attention in community ecology is degree of relatedness (summarised as the phylogenetic diversity, PD) of species (Cavender-Bares et al., 2009). In ecological studies, PD is often treated as indirect measure of FD, as taxa that are more closely related tend to show a higher ecological similarity than taxa that are distantly related (Harvey & Pagel, 1991) and they share traits necessary to persist environmental filters (Webb et al., 2002). Being independent on previously chosen ecological traits, PD as holistic characteristic of communities can (Cadotte et al., 2009) even outperform FD as measure. On the other hand, FD can be decoupled from PD (Devictor et al., 2010), e.g. if some functional traits are under strong stabilising selection (Prinzing et al., 2008) or re-evolve several times (Wake, 2009).

However, as most studies have used either FD or PD as measure, the correlation of both remains unclear for most communities and studies combining functional and phylogenetic characteristics of communities are required (Devictor et al., 2010).

*Community ecology & tropical amphibians* – Amphibians have been used as model organisms for community ecology in several studies. Especially anurans show high morphological and ecological diversity that makes them ideal for community studies (Wells, 2007). This is especially true in the tropics where diversity is much higher than in temperate zones (Duellman, 1999). Early (descriptive) studies on communities of adults anurans were performed in the 70s by Barbault, Crump, Duellmann, Inger & Colwell, and Toft (for references, see Wells, 2007, and chapter one). A basic summary of their and later studies is given in the introduction of chapter one.

The interest on these communities is, beside the high diversity, based on the fact that amphibians play an important role in many ecosystems (Whiles et al., 2006). This is also true for anuran tadpoles which can influence ecosystem structure and function (Kupferberg, 1997;

Flecker et al., 1999) and can act as keystone group (Holomuzki et al., 1994). Despite the ecological relevance of tadpoles, the shaping forces of tropical tadpole communities, especially those in streams, have long remained unexplored (Wells, 2007). After some pioneering studies in South-East Asia (e.g. Inger et al., 1986), most of the recent studies have been conducted in the neotropics (Brazil) (Eterovick & Barata, 2006; Afonso & Eterovick, 2007; Both et al., 2008). They generally show that different environmental factors influence tadpole communities. However, these communities are rather of poor species richness. Furthermore, beside the discussion of eco-morphological groups, FD has widely been ignored. Only recently quantitative phylogenetic measures were applied (Eterovick et al., 2010), however, so far no study quantified PD as characteristic of the whole community.

It is still not clear what rules the size and composition of tadpole communities. This especially applies to the very species rich communities. Tadpole communities are therefore an underused although promising tool to reveal rules of coexistence, the key to understand biodiversity.

## Aims, results & conclusions

The three main chapters of this work are all linked to the above described areas of community research. They are aimed to increase the knowledge on the performance of different measures of community diversity in general and on amphibian community structure and diversity in particular. Starting with the latter – the least general level – I face questions that have been attempted to be answered at times and have also recently been attracting herpetologist. There is an impressive diversity of adult frogs in tropical rainforest but also a concomitant large ecological overlap of many of these species. But where and how do they perform during their larval stage? Are there rules influencing larval (tadpole) communities, especially focussing environmental constraints and the possible role of competition?

I show that many frogs share breeding sites and that streams can play a major role for frog reproduction. I also show for the first time that there are habitat driven tadpole communities, i.e., specific habitat characteristics cause specifically assembled communities in streams. Often but not always closely related tadpoles belong to similar eco-morphological guilds, and this belonging is more important for microhabitat choice than taxonomic relations. In several parts of the studies I agree with other authors that competition is not of importance in naturally stream tadpole communities. In contrast, I can also evidence that competition can indeed have large influence on tadpole communities if taking inhospitable seasons into account.

At the more general ecological level, I transfer a question of recent ecological interest into primary freshwater habitat for the first time: do measures of diversity that refer to ecological functions provide more information than simply the number of species? If so, what is the

additional information and do these measures allow conclusions of shaping forces of communities?

Species richness (SR) is a valuable measure of diversity but it may lack important information. Using functional diversity (FD) as measure instead, I reveal patterns of functional redundancy, i.e., members of communities increasingly overlap in their ecological role with increasing SR. This finding is of particular interest as it originates from communities in primary freshwater habitat. I can also show that seasonal environmental changes of communities are non-random with respect to species function. Also phylogenetic diversity (PD), often treated as proxy for FD, is specifically influenced by seasonal environmental changes. However, I show that FD and PD are far from being convertible and that all three measures of diversity provide important information for community ecology studies.

*Species and eco-morphological guilds along environmental gradient*s – In **chapter one**, I start describing and analysing the ecology of the tadpoles of the different species occurring in rainforest streams in Ranomafana National Park (RNP, see below), Madagascar. I examined the relevance of streams for frog and tadpole diversity. Beside patterns of incidence and abundance of tadpoles, I assessed the influence of environmental factors on species distributions at two spatial scales: between and within streams. As, from an ecological point of view, the ecological role of a species is of higher importance than the species identity (Tilman, 2001), I increase the functional level and discuss the findings at the level of eco-morphological guilds.

I have detected tadpoles of 45 species by sampling exclusively in streams what equates to 44% of all frogs known from the study area. Considering only Mantellidae, an anuran family endemic to Madagascar (see below), I found 54% the species known from the study area. These percentages are considerably higher than in the neotropics, and comparable to South-East Asian rainforests. The total number of species found per community, reaching 22, is higher than reported in any other study from outside Madagascar. This underpins the importance of streams for frog reproduction, and therefore the importance of tadpole communities for the respective communities of adults on Madagascar. I can show that in general, and partly congruent to previous studies (Eterovick & Barata, 2006), the majority of species chooses similar types of streams for reproduction. I can also show that, in contrast to previous studies (Gascon, 1991), there are habitat driven, distinct species communities, i.e. that species composition is correlated with habitat characteristics. Based on the observed non-correlation of species distribution between and within streams, I conclude that competition is unlikely to act as shaping force in tadpole communities. I therefore support the assumption that eco-morphological adaptations

determine microhabitat choice within streams (Inger et al., 1986; Eterovick & Barata, 2006) and argue that these adaptations overlay the phylogenetic background of tadpoles.

*Species richness and functional diversity* – **Chapter two** also examines stream tadpole communities and their dependence on surrounding habitat. Here, however, I rather anonymise species, quantify diversity of communities as species richness (SR) on the one hand and functional diversity (FD) on the other hand, and analyse the interdependencies of both measures. I furthermore model random communities to compare observed values of FD with predictions from the random communities and, therefore, to statistically proof whether communities might be shaped by competition, environmental filters, or whether they assemble randomly. In contrast to chapter one, I use a continuous measure of FD rather than eco-morphological (functional) groups.
Using a different approach than in chapter one, I identify similar habitat characteristics as of importance for SR of stream tadpoles communities, namely stream size and velocity. Comparing SR and FD of communities, I identify patterns of functional redundancy, i.e., an overlap in ecological function of species especially in species rich communities. My results are in agreement with previous studies that show FD providing more information than SR (e.g., Petchey et al., 2007; Flynn et al., 2009), however, this study is of particular interest as it deals with communities in primary habitat. Additionally, it is the first study on FD of tadpole communities. As another main result, at least in the species rich tadpole communities, FD did not reach the values as predicted by random communities. This so called "low FD" indicates that environmental filters and surely not competition (Petchey et al., 2007) shape tadpole communities. I could therefore statistically proof the assumptions from chapter one and the few previous works (Inger et al., 1986; Eterovick & Barata, 2006).

*Importance of seasonality on processes structuring communities revealed by performance of three measures of diversity* – Like chapter two, **chapter three** is in general aimed at the comparison of different measures of diversity. Beside SR and FD, I also refer to phylogenetic diversity (PD) of stream tadpole communities. In contrast to the previous chapters and most comparable publications, I here treat communities not as being static, but as being recurringly changing due to the influence of annual climatic patterns (= seasons). Therefore, I here especially focus on how seasonality acts on SR, and how changes in SR are reflected in FD and PD, i.e., whether species appear and disappear randomly or not with respect to their ecological function (FD) and relatedness (PD).

I show that from the wet to the dry season, SR of tadpole communities decreases, as do FD and PD. Interestingly, FD and PD change differently from SR and also differently from predictions retrieved from random communities and simulated random changes. Contradictory at first glance, the loss of FD was less than predicted whereas the loss of PD was stronger than predicted. I found that communities in the dry season follow very different assembly rules than in the wet season and that, in contrast to previous studies including chapters one and two of this work, stream communities can be shaped by interspecific competition. I show that all three measures of diversity perform differently, all providing important information on communities and changes in community structure. I also highlight the importance of seasonality for community diversity, and therefore the need to include seasonality in community studies.

The chapters of this work are written as self-contained papers with a number of authors. My contributions and the contributions of the co-authors are stated in detail at the end of each chapter. In general, I have substantially contributed to the design and conduction the field work, have designed and conducted statistical analyses, and written the manuscripts.

## Addendum

The study system I used for research on community ecology consisted of a number of rainforest streams in Ranomafana National Park (RNP), Madagascar. RNP is located in the eastern escarpment of this island (Figure 1), which is widely known for its species richness and high degree of endemism (Myers et al., 2000), especially of anurans (Vieites et al., 2009) (Vieites et al., 2010). It covers a range of 43,500 ha, mainly composed of mid-elevational rain forest. Due to the mountainous/fissured topography this region is penetrated by a large number of different types of streams which can harbour very species rich tadpole communities. The water in the streams is clear, available substrates are rock, gravel, sand, and leaves. There is almost no vegetation in the streams.

In the following chapters I often refer to species names and their belonging to specific eco-morphological guilds and further traits used for FD calculations, respectively. I here provide an illustrative overview of some representative tadpoles of the eco-morphological guilds. I do not refer to tadpoles of species that breed outside streams, i.e. in ponds, phytotelmata, and terrestrial slime or foam nests. For several species, detailed tadpole descriptions are published or in progress; an overview on these publications is given in chapter one.

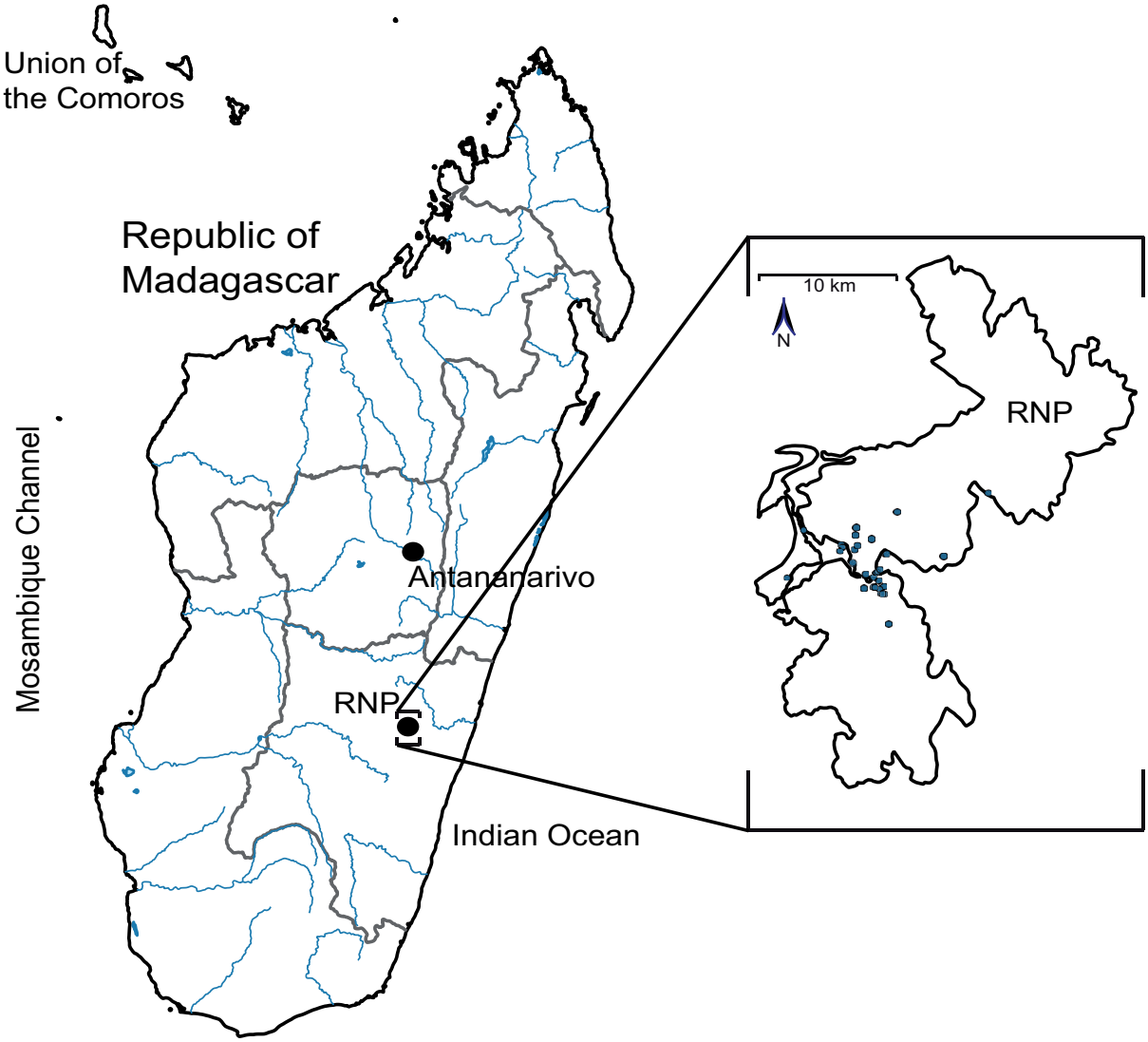


**Figure 1** Map of Madagascar showing the location of the Ranomafana National Park (RNP), grey borders mark districts, blue lines mark major water bodies, and an enlarged section showing RNP and sample sites as blue symbols. Madagascar map modified after "NordNordWest", licensed under CreativeCommons 3.0, RNP boundary is courtesy of J. Dempewolf.

Tadpoles of rainforest stream communities in Ranomafana national Park (RNP) all belong to four genera of the endemic family Mantellidae. The, in terms of tadpoles, two most common genera, *Boophi*s and *Mantidactylus*, consist of several types of tadpoles that can be summarised into eco-morphological guilds. In *Boophis*, subgenus *Boophis*, three guilds can be distinguished (but there are also intermediate ones). A range of species are unspecialised and form an eco-morphological guild named "*Boophis* – generalised". These tadpoles have a medium sized tail with well developed but not enlarged fins. The body is rounded and the oral disc is about 40 – 60% of body with, has well developed beak and keratodonts rows. We assigned tadpoles of 15 species sampled in rainforest streams of Ranomafana National Park (RNP) to this guild. Clear adaptations to running stream sections can be observed in tadpoles of the

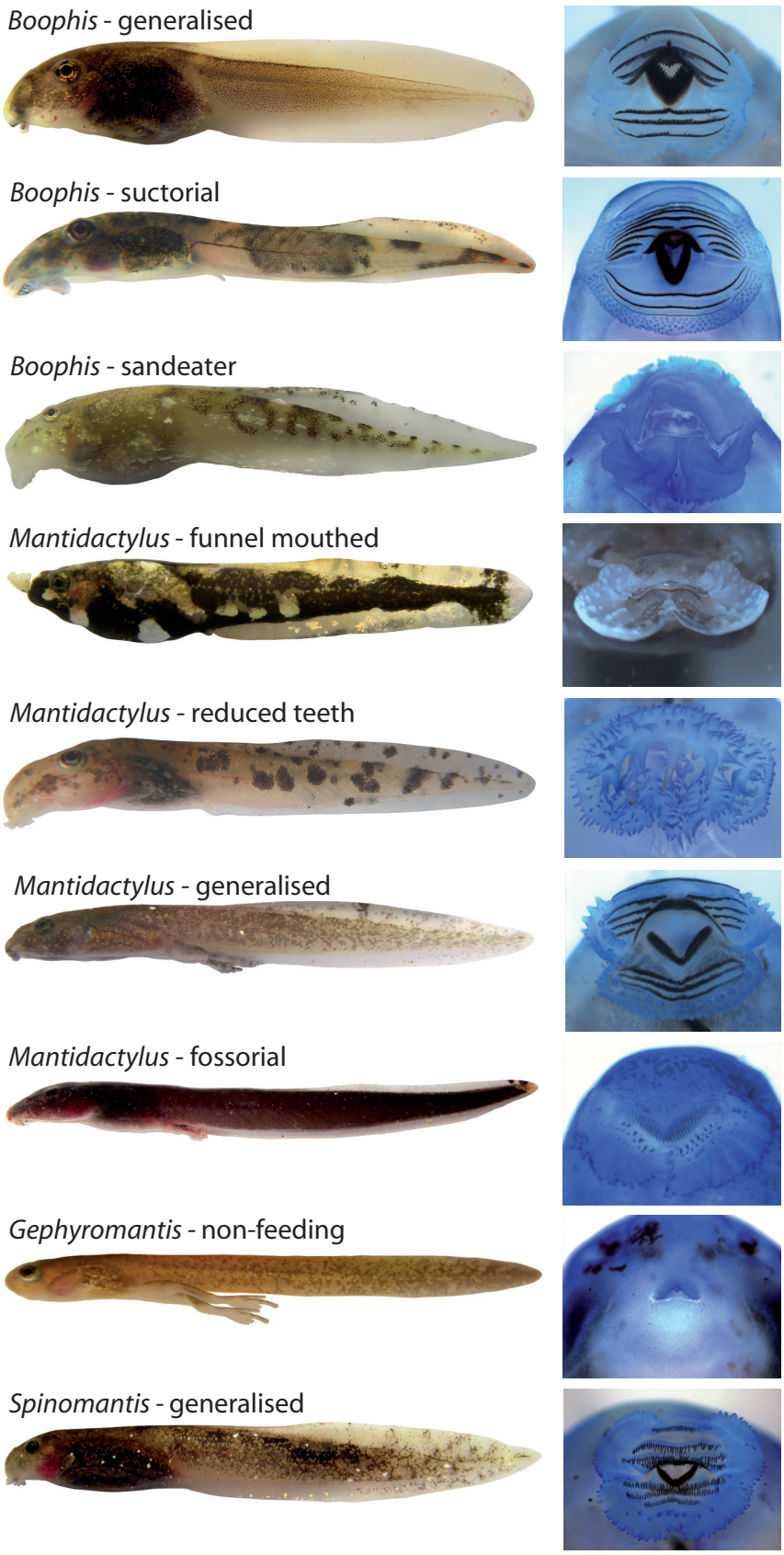


**Figure 2** Tadpoles exemplarily representing the eco-morphological guilds found in the stream communities of Ranomafana National Park. To each tadpole, a photography of the oral disc is shown. Oral discs are dyed by methylene blue to accentuate the non-keratinised oral disc structures, such as papillae and labia. The following species are displayed (top to bottom):
*Boophis periegetes*,
*B. schuboeae*,
*B. picturatus*,
*Mantidactylus* sp. 1,
*M. majori*,
*M.* sp. 28,
*M.* sp. 48,
*Gephyromantis sculpturatus* (oral disc: *G. tschenki*),
*Spinomantis fimbriatus*.

eco-morphological guild "*Boophis* – suctorial". These adaptations are strong tail musculature and reduced tail fins, a relative flat body and an oral disc being as wide as the whole body. Furthermore, the oral disc consists of a well developed beak, a high number of keratodonts rows and a high number of well developed papillae. Six species from RNP could be assigned to this guild. Another, quite different specialisation can be found in the eco-morphological guild "*Boophis* – sandeater". The most obvious characteristic is the absolute absence of any keratinised structure in the oral disc but oversized labia. There is only the tadpole of a single species showing this outstanding morphology in the Mantellidae: *B. picturatus*.

Further specialisation can be found in the eco-morphological guilds of the genus Mantidactylus. Here, the eco-morphological guilds generally fit the taxonomic classification of subgenera. The five species of the "*Mantidactylus* – funnel mouthed" (subgenus *Chonomantis*) are mainly characterised by their extended lower labium causing an umbelliform shape of the oral disc. A weak beak exists but in general there are no keratodonts. The tail is strong; the fins are of medium size. These tadpoles are morphologically very similar to each other and show a high variability in colouration within and between species. It is therefore almost impossible to distinguish tadpoles of these species without molecular methods. A review of tadpoles of the funnel mouthed *Chonomantis* is accepted for publication (Grosjean et al., in press).

The eco-morphological guild "*Mantidactylus* – reduced teeth (subgenus *Ochthomantis*) consists of species that have a rather generalised stream tadpole appearance, however, their oral disc is characterised by strong reductions of keratinised structures and further changes of other components. Within this guild, species can again be classified into three groups mainly due to oral disc modifications. A detailed description of the single species is submitted (Randrianiaina et al., submitted).

Tadpoles of the subgenus *Brygoomantis* belong to a rather generalised type, called "*Mantidactylus* – generalised". Beside some characteristics that are difficult to define, they mainly differ from other generalised eco-morphological guilds by their direction of the oral disc.

In RNP only a single member of "*Mantidactylus* – fossorial" (subgenus *Hylobatrachus*) occurs in the stream communities. This tadpole, currently at the status of a confirmed candidate species (CCS, Vieites et al., 2009) shows morphological adaptations that are often assigned to fossorial life. The tail is long, flat and has very small fins. The body is flattened and the keratodonts of two rows are elongated, the latter preventing sand intrusion in oral cavity.

Tadpoles of four of the species sampled in RNP belong to the genus *Gephyromantis* subgenera *Duboimantis* and *Laurentomantis*. All species have very pronounced modifications, i.e. a very thin and long tail almost without fin, a rather small body and only a diminutive oral disc opening.

The latter is an indication that tadpoles of this group are endotroph, i.e. non-feeding. For this reason this eco-morphological guild is named "*Gephyromantis* – non-feeding". The genus *Gephyromantis*, however, also consists of tadpoles showing a generalised body shape for stream breeding tadpoles with well developed oral disc structures. These at least partly carnivorous tadpoles do not occur in RNP.

Tadpoles of *Spinomantis* (eco-morphological guild named "*Spinomantis* – generalised") are often rather stout and have well developed tail and tail fins. Keratinised structures of the oral disc are developed but not very pronounced. Whereas they seem to be similar to *Boophis* – generalised at the first view, their oral disc is considerably smaller and consists of more soft structures than the one of *Boophis*.

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# Species distribution and community structure of anuran larvae in rainforest streams of Madagascar

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# Abstract

Tropical rainforests harbour a high number of frog species. Their tadpoles can form species rich and morphologically divers communities, particularly in streams. Tadpole diversity is probably important for ecological differentiation of species but it is poorly known how these communities are organised. Using information from Madagascar's remarkably species rich stream tadpole communities, we analysed the distribution of 44 species, and how they assemble in communities. Facing two functional and two spatial levels, we show that both rare and common species can be found in most eco-morphological groups of tadpoles. Habitat characters of the streams and surrounding forest influence species composition. Whereas there is a general trend in preferring wide, deep, and not steep streams for most species, some of the eco-morphological guilds separate along specific habitat characters. Also within streams, tadpoles partition microhabitat mainly according to their eco-morphological group but species dissimilarities on both spatial scales are not correlated. Morphological constraints seem to be more important than phylogenetic relations and there is no evidence that competition between tadpoles shapes their communities.

Keywords: Madagascar, Ranomafana National Park, Anura, tadpole, eco-morphological guild, community

# Background

Tropical anuran communities are impressively rich in species compared to those from temperate regions. One of the reasons is that frogs in the tropics exploit a wide range of niches both for foraging and reproduction (Wells, 2007). Most tropical frogs can broadly be divided into the distinct groups of arboreal frogs and leaf litter frogs (Wells, 2007), next to additional rarer groups such as fossorial and aquatic species. Beside the spatial partition of these groups, they can also vary in temporal activity (Duellman, 1978, 1989; Vitt & Caldwell, 1994; Parmelee, 1999; Wells, 2007; Glaw & Vences, 2007). Within the groups, however, species often show a broad ecological overlap. For instance, with exception of a few microphagous specialists, most leaf litter frogs are generalist feeders (Toft, 1980b, a, 1981; Parmelee, 1999; Vences et al., 1998; Vences & Kniel, 1998; Clark et al., 2005). Also members of communities of tropical riparian frogs, most of which also qualify as leaf litter frogs as they inhabit this terrestrial habitat next to streams, have a large

ecological overlap (Inger & Colwell, 1977), with some differences in the spatial use of microhabitats (Inger, 1969; Inger & Voris, 1993; Gillespie et al., 2004; Afonso & Eterovick, 2007a). Due to this high ecological similarity, it is assumed that species specific behavioural and/or physiological constraints rather than interspecific interaction determine habitat use and prevalence of tropical frogs (Ernst & Rödel, 2006; Afonso & Eterovick, 2007a).

A striking and important feature of tropical anuran communities, especially at higher elevations, is the establishment of specific reproductive strategies beside the common use of ponds. This includes for example direct development (Campbell, 1999; Duellman, 1999) and reproduction in streams (Wells, 2007). In fact, streams are used by a high percentage of rainforest frogs (Parris & McCarthy, 1999; Vences et al., 2008) and the assemblages show high morphological diversity (Wells, 2007). Diversification of reproductive modes and of tadpoles might thus be an important factor influencing amphibian community diversity.

The species richness of such a tropical tadpole community can be very high because many species can share same breeding sites (Heyer, 1973; Duellman, 1978; Inger et al., 1986; Aichinger, 1987; Gascon, 1991; Magnusson & Hero, 1991; Azevedo-Ramos et al., 1999).

The shaping forces of tropical tadpole communities, especially those in streams, have long remained unexplored (Wells, 2007). After some pioneering studies (Inger et al., 1986), more recent works have shown that, in tropical streams, the species richness of tadpoles is to a varying degree (and sometimes not) influenced by different environmental factors, such as stream size, velocity, light regime, temperature, predator abundance or vegetation cover (Parris & McCarthy, 1999; Eterovick & Barata, 2006; Afonso & Eterovick, 2007b; Both et al., 2008; Strauß et al., 2010). Characteristics of adult habitat (e.g., forest structure) may play a minor role (Strauß et al., 2010). In general, the composition of a tadpole community is primarily affected by breeding site selection of adults and less by tadpole success (Inger et al., 1986; Magnusson & Hero, 1991; Alford, 1999; Afonso & Eterovick, 2007b). Within the communities, tadpoles of some species show selectivity for microhabitats (Eterovick & Barata, 2006; Grosjean et al., in press; Randrianiaina et al., submitted), whereas these preferences are not necessarily rigid (Eterovick & Barros, 2003). There can be a high level of spatial niche overlap among species (Eterovick & Barros, 2003) indicating that in natural stream communities competition is not of importance (Inger et al., 1986; Eterovick & Barata, 2006; Strauß et al., 2010).

A special focus on tropical stream tadpole communities is justified as these larvae show greater morphological diversity than pond living tadpoles do (Wells, 2007), and a pronounced niche differentiation can therefore be expected. However, the role of this diversity in shaping anuran communities is not yet understood. The so far most species rich stream tadpole communities with up to 25 species per stream are found on Madagascar (Vences et al., 2008; Strauß et al.,

2010). Other communities in Brazil contain up to ten species per site (Hero et al., 2001; Eterovick, 2003; Eterovick & Barata, 2006; Afonso & Eterovick, 2007b). Madagascar in general is characterised by high species diversity, in particular of amphibians (Vieites et al., 2009), with new species being described continuously (e.g. Andreone et al., 2010; Glaw et al., 2010; Vences et al., 2010). Additionally, a large number of descriptions of tadpole morphology and ecology ecology have been published (e.g., Glos & Linsenmair, 2005; Altig & McDiarmid, 2006; Glos et al., 2007; Grosjean et al., in press) with some of these works significantly contributing to revisions of anuran systematics (e.g. Randrianiaina et al., 2009b; Randrianiaina et al., submitted). Despite this increase in knowledge on single species, the structure of Malagasy tadpole communities is largely understudied.

The species-rich tadpole communities of Ranomafana National Park (RNP) provide an excellent model for community studies. For RNP, which is located in the south-eastern escarpment of Madagascar, 112 species including 31 confirmed and unconfirmed candidate species have been reported (Vieites et al., 2009; Vences et al., 2010; Randrianiaina et al., submitted). RNP is located at mid-elevation and spans an altitudinal range of ca. 500-1500 m, and is characterized by high rainfall and absence of a completely dry season; all factors that correlate with high anuran species richness in tropics (Crump, 1971; Duellman, 1978; Péfaur & Duellman, 1980; Duellman, 1988, 1999).

Anurans of RNP have a high reproductive diversity (for a summary, see Glaw & Vences, 2007). All species have external fertilisation but the whole mantellid subfamily Mantellinae has a special reproductive behaviour without mating amplexus. Eggs are deposited in the water (lentic and lotic in the mantellid subfamily Boophinae and exclusively lentic by the the mantellid subfamily Laliostominae, the microhylid subfamily Scaphiophryninae, and the familes Hyperoliidae and Ptychadenidae or outside the water (Mantellinae and some microhylids). Egg deposition outside of the water can be on the forest floor close to water (most *Mantidactylus*, most *Mantella*, *Blommersia sarotra*), on leaves and rocks above water or in phytotelmata (*Guibemantis*, *Blommersia*, *Mantidactylus*). Some nidicolous species place eggs in tree holes, bamboo nodes and phytotelmata (*Anodonthyla*, *Cophyla*, *Platypelis*, and *Plethodontohyla*) or establish foam or slime nests on the forest floor (*Gephyromantis* sp. aff. *blanci*, *Stumpffia*, *Plethodontohyla*).

Tadpoles in RNP show great morphological diversity which can ecologically be interpreted as functional diversity (Strauß et al., 2010). They range from a "generalised" type (Altig & McDiarmid, 1999) to a variety of specialisations, such as enlarged oral discs with increased numbers of papillae and labial tooth rows, and with strong and flat bodies (i.e. adaptations to high water current, Glos et al., 2007), various kinds of reduction of oral disc structures (Altig & McDiarmid, 2006; Randrianiaina et al., submitted), funnel mouthed tadpoles (Grosjean et al., in

press) and non-feeding (endotrophic) nidicolous tadpoles (Randrianiaina et al., unpublished). All these kinds of tadpoles can co-occur in the same streams. Due to the high community species richness based on an even larger species pool in that area, and the high diversity of eco-morphological guilds, they represent a good opportunity to study fundamental principles of the assembly and structure of tropical communities.

Based on a comprehensive data set from streams in RNP we here analyse tadpole incidence, abundance, and habitat use, at different spatial scales and at the level of species and eco-morphological groups. The general aim of this study is to identify general patterns of habitat-tadpole and tadpole-tadpole relations, and to interpret these in an ecological and evolutionary context. We compare the distribution of tadpole species both at the level of species and eco-morphological guilds, and relate species distribution patterns to habitat variables on two spatial scales. At a broader spatial scale (between streams), we test whether species, morphological guilds, and communities (composition and structure) are associated with specific habitat variables, including the distribution of other tadpole species (as potential competitors). At a smaller scale (within streams), we investigate the spatial differentiation between stream microhabitats, again at the level of species and eco-morphological guilds.

# Methods

### Study sites

We conducted this study in the Ranomafana National Park (RNP) in the south eastern escarpment of Madagascar. RNP ranges from 500 m to 1,500 m a.s.l. and covers an area of 43,500 ha, mainly composed of mid-elevational rain forest. Due to the mountainous/fissured topography this region is penetrated by a large number of different types of streams that are used by frogs for reproduction. There are only few stagnant waterbodies available. So far, in RNP 107 species of frogs have been recorded (Vieites et al., 2009). Our study sites were distributed west of Ranomafana village and covered an elevational range of ca. 720 to 1,170 m a.s.l. In this area 92 species of frogs have been recorded previously (Table 2) (Vieites et al., 2009).

### Species sampling

In this study area, we repeatedly sampled 29 study sites in the wet season 2007 (February to March) and 2008 (January to February) plus four additional streams in 2008 (Table 1). Each study site represents a stream section of 30 m length and its surrounding habitat. There was no direct

link between any two sites so that no tadpoles could be washed from one site into another. We chose stream sections with differing characteristics (e.g., stream width, depth, structure, microhabitats) in a similar number. We sampled these sections for tadpoles using dip nets of different sizes and materials, adjusted to obtain optimal sampling results for each stream. Depending on stream width a varying number of people started sampling downstream and processed slowly upstream. We predefined eight types of microhabitat (see below), and kept tadpoles separately for each microhabitat. We carried tadpoles alive into the laboratory, euthanized them by immersion in chlorobutanol solution, and immediately sorted them into series based on their morphology. From each series, we identified one specimen by DNA barcoding based on a fragment of the mitochondrial *16S* rRNA gene (Vences et al., 2005; Vences et al., 2008). DNA sequences of all 3132 identified tadpole series (1472 from 2007 and 1660 from 2008; corresponding to 43 species, 2-22 species per stream) are deposited in Genbank (accession numbers FJ217329-FJ217345, GQ904717-GQ904746, GU808474-GU808492, GU974370-GU975745; further sequences are in the process of preparation for submission to Genbank).

Attempts were made to classify tadpoles into eco-morphological guilds (Altig & Johnston, 1989; Raharivololoniaina et al., 2006; Randrianiaina et al., 2009a). For this study, we have decided to define these guilds based on body and oral disc morphology (Altig & McDiarmid, 1999). We chose a scale that, with some exception in the eco-morphological guilds of *Boophis*, fits phylogenetic groups (e.g., subgenera). Species names, their phylogenetic group and their assignment to eco-morphological guild can be found in Table 2 and Table 3.

**Table 1** Study sites (streams) sampled for tadpoles during this study. Streams are listed with their local names in alphabetical order, with the 29 repeatedly sampled streams first followed by the 4 streams additionally sampled in 2008. GPS datum is WGS84.

| Study site | S (hddd°mm.mmm°) | E (hddd°mm.mmm°) | altitude (m a.s.l.) |
|---|---|---|---|
| Ambatolahy II | 21°14.468' | 47°25.591' | 965 |
| Ambatolahy III | 21°14.464' | 47°25.624' | 973 |
| Ambatovory (Barrage) | 21°13.862' | 47°25.436' | 1028 |
| Ambodiamontana | 21°15.249' | 47°25.197' | 935 |
| Ankerana (Belle Vue) | 21°15.582' | 47°25.320' | 963 |
| Bevoahazo | 21°11.898' | 47°29.721' | 722 |
| Bibiango Old Bridge | 21°15.442' | 47°25.099' | 961 |
| E100 | 21°15.806' | 47°25.510' | 949 |
| Fompohonina River | 21°16.106' | 47°25.483' | 972 |
| Fompohonina II | 21°16.075' | 47°25.421' | 950 |
| Fompohonina III | 21°15.907' | 47°25.349' | 1012 |
| Fompohonina IV | 21°16.110' | 47°25.546' | 982 |
| Imaloka | 21°14.529' | 47°27.938' | 957 |
| Kidonavo | 21°13.540' | 47°22.210' | 1147 |
| Mariavaratra | 21°15.806' | 47°25.135' | 955 |
| P100 | 21°15.840' | 47°25.098' | 982 |
| Ranomena | 21°12.736' | 47°26.010' | 1144 |
| Sahamalaotra Bridge | 21°14.113' | 47°23.767' | 1144 |
| Sahamalaotra Farihin-dRakotomainty | 21°14.216' | 47°23.810' | 1124 |
| Sahamalaotra Small | 21°14.366' | 47°23.709' | 1138 |
| Sahateza Pond Donald | 21°15.476' | 47°21.583' | 1147 |
| Sakaroa River | 21°15.889' | 47°24.730' | 930 |
| Talatakely Piste X175 | 21°15.846' | 47°25.161' | 966 |
| Up the waterfall | 21°15.315' | 47°24.767' | 1055 |
| ValBio stream | 21°15.191' | 47°25.271' | 929 |
| Vatoharanana | 21°17.338' | 47°25.765' | 1016 |
| Vatolampy I | 21°14.874' | 47°24.267' | 1084 |
| Vatolampy II | 21°14.833' | 47°24.229' | 1080 |
| Waterfall II | 21°15.117' | 47°25.348' | 930 |
| Atatatra I | 21°13.399' | 47°24.346' | 1121 |
| Atatatra II | 21°13.710' | 47°24.347' | 1121 |
| Sahafarihana I | 21°14.315' | 47°24.320' | 1166 |
| Sahafarihana II | 21°14.133' | 47°24.429' | 1123 |

## Habitat variables

To analyse breeding site choice of frogs we recorded the following types of habitat variables: (1) characteristics of the surrounding forest that may be of relevance for frogs, (2) structure of riparian vegetation, which can be used for breeding activities and (3) general characteristics of the stream. To analyse microhabitat preferences of tadpoles we recorded (4) the frequency of eight predefined microhabitats (see below).

In detail, we recorded forest habitat characteristics on four circular plots of 6 m in diameter, equally distributed along the 30 m stream section and their midpoint being in a distance of 7 m to

the stream edge. The variables were the number of shrubs (≤ 5 cm stem diameter at eye level) and the number of trees (> 5 cm diameter), canopy cover (%; estimated), and leaf litter depth (cm; measured at 4 points and averaged). To record habitat features of the stream sections, we laid transects consisting of adjoining 1×1 m quadrates crossing the stream perpendicularly. Starting at the downstream end of the sampling section, we recorded stream variables of 10 of those diagonal transects at intervals of 2 m, thus covering 33 % of the area of the sampling section. We recorded stream width (m) in the centre of each of these transects, and averaged. Stream velocity was analysed by measuring the stream *slope* (m), i.e. the difference in altitude between the upstream and the downstream end of the 30 m stream section. We recorded in each 1×1 m quadrate the stream depth, the stream canopy cover (coded as 0 = absent and 1 = present, and averaged), and the frequency of each of the eight microhabitat types (%). We defined microhabitat types based on ground substrate: leaves (organic material), sand (very finely grained up to ~3 mm grain size), gravel (grain size 3 mm to 25 cm), and rock (> 25 cm), separated for running (fast) and almost stagnant (slow) parts of the stream.

For additional data, tadpoles were opportunistically sampled in ponds and tree holes in the study area.

## Statistical analysis

*Species incidence and abundance* – We mainly evaluated graphically the incidence (percent of sampled streams occupied) and abundance (mean number of specimens of a species in sites where the respective species was found) of tadpoles in the streams studied. To test for reproducibility between years, we firstly plotted tadpole incidence and abundance in 2007 against 2008 (Appendix Figure 1 and Appendix Figure 2). Secondly, data of both years were averaged to compare incidence and abundance data of each species (Figure 3). To test for statistical significance of the incidence-abundance relationship, we applied linear mixed effects models (lme) on the original, non-averaged data. As our data consisted of repeated measures of species incidence and abundance (i.e., 2007 and 2008) and were therefore not independent data, lme allowed including random factors to avoid pseudoreplication. We started with a full model with abundance as dependent variable and incidence, year, and interactions as fixed effects. For random effects, species identity was nested within year. We reduced the number of fixed effects until the minimum AIC was reached (Burnham & Anderson, 2002). We used F-tests to estimate p-values of the remaining terms.

To test whether the results are strongly influenced by rare species, we split the dataset into two parts of equal size. We chose this cut off in order to avoid an arbitrary cut off incidence value. Species were sorted according to their mean incidence of both years. The first data set included

the 22 species with high incidence (> 10% of the streams), the second data set included 21 species with low incidence (< 10% of the streams). We analysed only the first data set and applied lme as described above.

*Eco-morphological guild incidence and abundance* – To focus on eco-morphological guilds of tadpoles rather than on species identity, in a first step we graphically analysed the frequency of different incidence values, and marked each data point according to its eco-morphological guild (Figure 1). In a second step, we applied a similar procedure to the frequency of different abundance data. We grouped abundance data in steps of five specimens (Figure 2).

*Species-habitat associations* – To relate species occurrence to habitat variables, we used two different approaches. Firstly, we related species incidence to variables of the surrounding habitat and of the stream. For this analysis we used incidence values (presence-absence) because abundance data of tadpoles may rather depend on reproductive strategy (e.g. clutch size) than on breeding site choice. Secondly, we used relative abundance of tadpoles within streams to calculate microhabitat preferences of tadpoles. Species and eco-morphological guilds were then compared based on their microhabitat preferences.

*Tadpole incidence: breeding site choice* – To test for differences in species composition between years, we calculated stream-species distance matrices based on presence and absence of species using Bray-Curtis-distance, also known as Sørensen index. We subsequently performed a Mantel test based on Pearson's product-moment correlation implemented in the vegan library (Oksanen et al., 2009) using 9999 permutations. This test was based on the 29 streams sampled repeatedly in both years. Community similarity did not significantly differ between years (Mantel statistics $r = 0.701$, $p < 0.001$; highly correlated). Accordingly, we used only data of 2008 for all further analyses of species habitat-associations ($n = 33$).

We tested whether there is a general correlation of tadpole species composition and habitat variables. Thus, we calculated a stream-species distance matrix based on presence and absence of species using Bray-Curtis-distance, a stream-habitat distance matrix of the same streams using Euclidean distance and performed a Mantel test as above.

To analyse incidence-habitat associations and therefore breeding site choice, we included only species in the analysis that were found in at least seven streams in 2008 in order to have sufficient data for each species. Rare species (i.e., incidence $\leq 0.18$) can hardly be associated to habitat variables due to their absence at too many sites, and they were therefore excluded from all subsequent analyses. The same is also true for species occurring in almost all streams and therefore all habitat types. However, due to their general presence, we included these species in the RDA plots (see below).

Redundancy analysis (RDA) is a constrained (therefore non-symmetric) ordination method, i.e., it deals with an independent data set (i.e., habitat variables) and a dependent data set (i.e., tadpole community data). RDA is related to Principal Component Analysis (PCA) and is based on Euclidean distance and performs linear mapping. We used this statistical procedure to compare a stream habitat matrix with a stream species-incidence matrix. Because outliers can affect the outcome of the RDA, we reduced their influence by applying box-cox-power-transformations (Box & Cox, 1964) on habitat variables containing outliers. We evaluated pair-plots to test that there are no obvious non-linear relations in the habitat variables.

The results of RDA were plotted to evaluate patterns of species co-occurrence and their relation to habitat variables. Additionally, we performed a cluster analysis according to species data and methods used for RDA and plotted species clusters in the RDA output; original results of cluster analysis are provided in Appendix Figure 3.

*Tadpole microhabitat preferences* –We calculated microhabitat preferences using Ivlev's electivity index (E, Ivlev, 1961). For this, the relative distribution of all tadpoles of a species in a stream is compared with the frequency of the eight predefined microhabitat categories. If a higher proportion of tadpoles is found in a microhabitat than would have been expected by a random tadpole distribution, $E$ of this species for this microhabitat will be positive. If the observed occurrence is low compared to a random tadpole distribution, $E$ will be negative. $E$ ranges from −1 (complete avoidance) to +1 (complete preference). If an available microhabitat is not used at all, the index will be −1. If a species is present only with very few specimens in a stream, such an absolute avoidance value is automatically assigned to some microhabitats. As we can not proof whether this reflects true preferences/avoidances or whether it is an artefact due to low abundances, for each species we used only those streams where it was present with at least 8 specimens to provide the theoretical opportunity to be present in all microhabitats. As a result, species that were (locally) rare were not used in this analysis. Of the 41 species found in 2008, only 24 showed sufficient abundances to analyse microhabitat preferences. For each species, we calculated Ivlev's electivity index for all the streams with sufficient abundance of the respective species and averaged.

We constructed a species microhabitat-preference matrix. We performed principal component analyses (PCA) on all 8 microhabitat preferences for the 24 remaining species on the correlation matrix in order to standardise for the influence of unequal variance. The original data were evaluated for matching the requirements of a PCA as described above for RDA. To reduce the influence of outliers, we applied box-cox-power-transformations (Box & Cox, 1964). We estimated the number of meaningful PCs by a scree plot (Zuur et al., 2007). The results were graphically evaluated using PCA biplot.

For a better interpretation of both, breeding site choice and microhabitat preferences, and to reveal structuring processes like competition, we compared (dis-)similarity of species regarding their breeding-site-choice on the one hand and regarding their microhabitat choice on the other hand. If for example species with similar general ecological requirements choose the same streams for reproduction but tadpoles face competition, these may use different microhabitats and dissimilarities for breeding site choice and dissimilarities for microhabitat preferences will be negatively correlated. If on the contrary breeding site choice depends on adult ecology, and tadpole microhabitat preferences depend on tadpole ecology, no correlation will be found. For both spatial scales of habitat partition we calculated distance matrices (due to negative values for microhabitat data, we used Euclidean distances) and performed Mantel tests as described above. We only included species that were previously used for breeding site choice analyses as well as for microhabitat use analyses.

We performed all statistical analysis in the R environment (R Development Core Team, 2009) using the following packages: car (Fox, 2008), lattice (Sarkar, 2008), lme4 (Bates & Maechler, 2010), MASS (Venables & Ripley, 2010), prabclus (Henning & Hausdorf, 2009), and vegan (Oksanen et al., 2009).

# Results

### Species diversity

Of the total of 107 species recorded from RNP (confirmed and unconfirmed candidate species, CCS and UCS, are here referred to as species as well, Vieites et al., 2009) our study focuses on those of the family Mantellidae of which the majority breeds in streams. No tadpoles of the Ptychadenidae (1 species in RNP), Hyperoliidae (2 species), or Microhylidae (15 species) were found in the streams studied; these frogs all reproduce either in lentic water bodies or are nidiculous with non-feeding tadpoles. We made only occasional observations of microhylid larvae in ponds (e.g., *Paradoxophyla palmata*) or tree holes (*Platypelis grandis*, *Plethodontohyla mihanika*).

In the streams we found tadpoles of 44 out of 81 mantellid species present in the RNP study area. Of the adult Mantellidae reported by Vieites et al. (2009) based on a long year dataset, larvae of 37 were found during the survey. Additionally, 7 species were found, including 5 species that have not been known to science (see e.g. Grosjean et al., in press; Randrianiaina et al., submitted). Furthermore, we made occasional observations of eggs or tadpoles of four more mantellid

species in ponds and jelly nests. Tadpole communities were species-rich, with up to 18 species per stream in 2007 and up to 22 species per stream in 2008.

Within the Mantellidae, the most prominent genus in RNP larval communities is *Boophis*. In the adult stage these are treefrogs, characterised by large eyes and enlarged discs on fingers and toes. *Boophis* is divided into two subgenera, *Boophis* and *Sahona*. The latter, in RNP present with only three species, deposit eggs in ponds. We found no tadpoles of this subgenus in streams, but tadpoles of one species in a pond at the local main road. Vieites et al. (2009) reported the presence of 26 species of the subgenus *Boophis* in this part of RNP. Of those, we found 16 species plus 6 more species that were not reported from this area before. Out of these six species, 2 were not known to science before.

The second genus strongly represented in RNP stream tadpole communities is *Mantidactylus*. These are largely leaf litter frogs that belong to the subfamily Mantellinae and are characterised by the deposition of eggs outside of the water. *Mantidactylus* is divided into various subgenera which strongly differ in tadpole morphology and of which five are present in RNP: (1) The semi-aquatic frogs of *Brygoomantis* place their egg clutches on the forest floor, and the (generalised) tadpoles are washed with rain into the streams. Four species are reported from RNP. (2) The "funnel mouthed" tadpoles of the subgenus *Chonomantis* are represented with seven species. (3) A single species of the subgenus *Hylobatrachus* is known from Ranomafana thus far (Vieites et al., 2009), and the highly specialized tadpoles of this species (Altig & McDiarmid, 2006) were also sampled during this study. (4) The subgenus *Ochthomantis*, with its tadpole morphology and phylogeny recently revised (Randrianiaina et al., submitted), was expected to be present with 3 species (Vieites et al., 2009), of which we could find all tadpoles. We also sampled tadpoles of a further species that was not known to science before (Randrianiaina et al., submitted). (5) Adults of *M. grandidieri*, one of the largest frogs of Madagascar and a representative of the subgenus *Mantidactylus*, were observed at some of the study sites, we did not find tadpoles of this species.

The genus *Spinomantis* includes both arboreal and more terrestrial species. Six *Spinomantis* species were listed for this area in RNP of which we found three in the streams.

RNP harbours two species of *Mantella*, *M. madagascariensis* and *M. baroni*. Despite the fact that especially *M. baroni* is commonly encountered calling along streams (Glaw & Vences, 2007), we only found very few *Mantella* tadpoles.

Members of four subgenera of the genus *Gephyromantis* are present in RNP. The subgenus *Gephyromantis* is assumed to be reproductively independent from water and may have direct development (Glaw & Vences, 2007). We found a single jelly nest in the forest leaf litter, inhabiting tadpoles probably belonging to *G.* sp. aff. *blanci*, and therefore could confirm the

independence from water but contradict direct development (Randrianiaina et al., unpublished). In the streams studied. We found tadpoles of species assigned to the subgenera *Laurentomantis* and *Duboimantis*. These tadpoles have strongly reduced mouthparts and probably are non-feeding (Randrianiaina et al., unpublished). Whether they are accidentally washed into the streams by heavy rains or are a true part of the stream tadpole communities is unclear.

The arboreal frogs of the genus *Guibemantis* deposit their eggs on leaves and rocks over ponds and swamps (subgenus *Guibemantis*) or at phytotelmata of *Pandanus* screw pines (most species of the subgenus *Pandanusicola*). The latter group includes species that secondarily lost this way of reproduction (Glaw & Vences, 2007). Of these, we found tadpoles of one species (*Guibemantis liber*) in a very slow moving stream.

**Table 2** List of Mantellidae recorded for Ranomafana National Park ("adults") and their status (SP =described species, CCS =confirmed candidate species, UCS = unconfirmed candidate species, DCL = deep conspecific lineage) (Vieites et al., 2009; Glaw et al., 2010; Vences et al., 2010) and observed during our study. Given are the valid names and names used in previous publications, if applicable.

| Genus | Subgenus | Species group | Species | Status | Adults | Tadpoles 2007 | Tadpoles 2008 |
|---|---|---|---|---|---|---|---|
| *Boophis* | *Boophis* | *albilabris* | *Boophis albilabris* | SP | yes | yes | yes |
| *Boophis* | *Boophis* | *albipunctatus* | *Boophis* sp. 18 = "*ankaratra*" | CCS | no | yes | yes |
| *Boophis* | *Boophis* | *albipunctatus* | *Boophis schuboeae* | SP | yes | yes | yes |
| *Boophis* | *Boophis* | *albipunctatus* | *Boophis luciae* = sp. 17 = aff. *sibilans* | SP | yes | yes | yes |
| *Boophis* | *Boophis* | *goudoti* | *Boophis madagascariensis* | SP | yes | yes | yes |
| *Boophis* | *Boophis* | *goudoti* | *Boophis periegetes* | SP | yes | yes | yes |
| *Boophis* | *Boophis* | *goudoti* | *Boophis reticulatus* | SP | yes | yes | yes |
| *Boophis* | *Boophis* | *goudoti* | *Boophis* sp. 8 = aff. *rufioculis* | CCS | yes | yes | yes |
| *Boophis* | *Boophis* | *goudoti* | *Boophis obscurus* = sp. 13 = aff. *periegetes* | SP | yes | yes | yes |
| *Boophis* | *Boophis* | *goudoti* | *Boophis spinophis* = sp. 15 = *Boophis* sp. | SP | yes | no | no |
| *Boophis* | *Boophis* | *goudoti* | *Boophis* sp. 16 = aff. *boehmei* | SP | yes | yes | yes |
| *Boophis* | *Boophis* | *goudoti* | *Boophis* sp. 42 = aff. *goudoti* | UCS | no | yes | yes |
| *Boophis* | *Boophis* | *luteus* | *Boophis andohahela* | SP | yes | yes | yes |
| *Boophis* | *Boophis* | *luteus* | *Boophis elenae* | SP | yes | yes | yes |
| *Boophis* | *Boophis* | *luteus* | *Boophis luteus* (Andohahela) | SP (DCL) | yes | yes | yes |
| *Boophis* | *Boophis* | *luteus* | *Boophis sandrae* = sp. 22 = aff. *elenae* | SP | yes | no | no |
| *Boophis* | *Boophis* | *luteus* | *Boophis* sp. 37 = aff. *elenae* | UCS | no | yes | no |
| *Boophis* | *Boophis* | *majori* | *Boophis majori* | SP | yes | yes | yes |
| *Boophis* | *Boophis* | *majori* | *Boophis marojezensis* | SP | yes | yes | yes |
| *Boophis* | *Boophis* | *majori* | *Boophis picturatus* | SP | yes | yes | yes |
| *Boophis* | *Boophis* | *majori* | *Boophis* sp. 35 = aff. *majori* "long calls" | CCS | yes | yes | yes |
| *Boophis* | *Boophis* | *mandraka* | *Boophis* cf. *mandraka* | SP | yes | no | no |
| *Boophis* | *Boophis* | *mandraka* | *Boophis* sp. 38 = aff. *sambirano* | UCS | no | yes | no |
| *Boophis* | *Boophis* | *microtympanum* | *Boophis microtympanum* | SP | yes | no | no |
| *Boophis* | *Boophis* | *microtympanum* | *Boophis rhodoscelis* | SP | yes | no | yes |
| *Boophis* | *Boophis* | *microtympanum* | *Boophis piperatus* = sp. 30 = aff. *rhodoscelis* "Ranomafana" | SP | yes | no | no |
| *Boophis* | *Boophis* | *rappiodes* | *Boophis bottae* | SP | yes | no | no |
| *Boophis* | *Boophis* | *rappiodes* | *Boophis lilianae* | SP | yes | no | no |
| *Boophis* | *Boophis* | *rappiodes* | *Boophis rappiodes* | SP | yes | no | no |
| *Boophis* | *Boophis* | *rappiodes* | *Boophis tasymena* | SP | yes | yes | yes |

| Genus | Subgenus | Species group | Species | Status | Adults | Tadpoles 2007 | Tadpoles 2008 |
|---|---|---|---|---|---|---|---|
| *Boophis* | *Boophis* | *rappiodes* | *Boophis viridis* | SP | yes | no | no |
| *Boophis* | *Sahona* | *tephraeomystax* | *Boophis guibei* | SP | yes | no | no |
| *Boophis* | *Sahona* | *tephraeomystax* | *Boophis pauliani* | SP | yes | no | no |
| *Boophis* | *Sahona* | *tephraeomystax* | *Boophis tephraeomystax* | SP | yes | no | no |
| *Aglyptodactylus* | no | no | *Aglyptodactylus madagascariensis* | SP | yes | no | no |
| *Aglyptodactylus* | no | no | *Aglyptodactylus* sp. 3 = aff. *madagascariensis* "Ranomafana" | CCS | yes | no | no |
| *Blommersia* | no | no | *Blommersia blommersae* | SP | yes | no | no |
| *Blommersia* | no | no | *Blommersia domerguei* | SP | yes | no | no |
| *Blommersia* | no | no | *Blommersia* sp. 9 = aff. *sarotra* "Ranomafana" | CCS | yes | no | no |
| *Gephyromantis* | *Duboimantis* | no | *Gephyromantis* cf. *asper* | SP | yes | no | no |
| *Gephyromantis* | *Duboimantis* | no | *Gephyromantis plicifer* | SP | yes | no | yes |
| *Gephyromantis* | *Duboimantis* | no | *Gephyromantis sculpturatus* | SP | yes | yes | yes |
| *Gephyromantis* | *Duboimantis* | no | *Gephyromantis tschenki* | SP | yes | yes | no |
| *Gephyromantis* | *Gephyromantis* | no | *Gephyromantis blanci* | SP | yes | no | no |
| *Gephyromantis* | *Gephyromantis* | no | *Gephyromantis* cf. *boulengeri* | SP (DCL) | yes | no | no |
| *Gephyromantis* | *Gephyromantis* | no | *Gephyromantis enki* | SP | yes | no | no |
| *Gephyromantis* | *Gephyromantis* | no | *Gephyromantis runewsweeki* | SP | yes | no | no |
| *Gephyromantis* | *Gephyromantis* | no | *Gephyromantis* sp. 9 = *decaryi* | CCS | yes | no | no |
| *Gephyromantis* | *Laurentomantis* | no | *Gephyromantis ventrimaculatus* | SP | yes | yes | yes |
| *Gephyromantis* | *Laurentomantis* | no | *Gephyromantis* sp. 13 = aff. *malagasius* "Andasibe" | CCS | yes | no | no |
| *Guibemantis* | no | no | *Guibemantis liber* | SP (DCL) | yes | yes | no |
| *Guibemantis* | no | no | *Guibemantis pulcher* | SP | yes | no | no |
| *Guibemantis* | no | no | *Guibemantis depressiceps* | SP | yes | no | no |
| *Guibemantis* | no | no | *Guibemantis tornieri* | SP | yes | no | no |
| *Guibemantis* | no | no | *Guibemantis* sp. 7 = aff. *bicalcaratus* "South" | UCS | yes | no | no |
| *Guibemantis* | no | no | *Guibemantis* sp. 12 = aff. *bicalcaratus* "Manongarivo" | UCS | yes | no | no |
| *Mantella* | no | no | *Mantella baroni* | SP | yes | no | yes |
| *Mantella* | no | no | *Mantella madagascariensis* | SP | yes | no | no |
| *Mantidactylus* | *Brygoomantis* | no | *Mantidactylus alutus* | SP | yes | no | no |
| *Mantidactylus* | *Brygoomantis* | no | *Mantidactylus betsileanus* | SP | yes | no | yes |
| *Mantidactylus* | *Brygoomantis* | no | *Mantidactylus* sp. 24 = aff. *biporus* "Ranomafana" | CCS | yes | yes | yes |
| *Mantidactylus* | *Brygoomantis* | no | *Mantidactylus* sp. 28 = aff. *betsileanus* "slow calls" | CCS | yes | yes | yes |
| *Mantidactylus* | *Chonomantis* | no | *Mantidactylus melanopleura* | SP | yes | yes | yes |
| *Mantidactylus* | *Chonomantis* | no | *Mantidactylus delormei* | SP | yes | no | no |
| *Mantidactylus* | *Chonomantis* | no | *Mantidactylus* sp. 1 = *aerumnalis* | CCS | yes | yes | yes |
| *Mantidactylus* | *Chonomantis* | no | *Mantidactylus* sp. 4 "Maharira" = *charlottae* = cf. albofrenatus | UCS | yes | no | yes |
| *Mantidactylus* | *Chonomantis* | no | *Mantidactylus opiparis* | SP | yes | no | no |
| *Mantidactylus* | *Chonomantis* | no | *Mantidactylus* sp. 58 = *opiparis* | UCS | no | yes | yes |
| *Mantidactylus* | *Chonomantis* | no | *Mantidactylus* sp. 59 | SP | no | yes | yes |
| *Mantidactylus* | *Hylobatrachus* | no | *Mantidactylus* sp. 48 = aff. *cowanii* "small" = cf *lugubris* | CCS | yes | yes | yes |
| *Mantidactylus* | *Mantidactylus* | no | *Mantidactylus grandidieri* | SP | yes | no | no |
| *Mantidactylus* | *Ochthomantis* | no | *Mantidactylus femoralis* | SP | yes | yes | yes |
| *Mantidactylus* | *Ochthomantis* | no | *Mantidactylus majori* | SP | yes | yes | yes |
| *Mantidactylus* | *Ochthomantis* | no | *Mantidactylus* sp. 47 = aff. *mocquardi* "Ambatolahy" | CCS | yes | yes | yes |
| *Mantidactylus* | *Ochthomantis* | no | *Mantidactylus* sp. aff. *mocquardi* "Namorona" | CCS | no | no | yes |
| *Spinomantis* | no | no | *Spinomantis aglavei* | SP | yes | yes | yes |
| *Spinomantis* | no | no | *Spinomantis elegans* | SP | yes | no | no |
| *Spinomantis* | no | no | *Spinomantis peraccae* | SP | yes | yes | yes |
| *Spinomantis* | no | no | *Spinomantis* sp. 2 = *fimbriatus* | UCS | yes | yes | yes |
| *Spinomantis* | no | no | *Spinomantis* sp. 7 = *bertini* | UCS | yes | no | no |
| *Spinomantis* | no | no | *Spinomantis* sp. 8 = aff. *bicalcaratus* | CCS | yes | no | no |

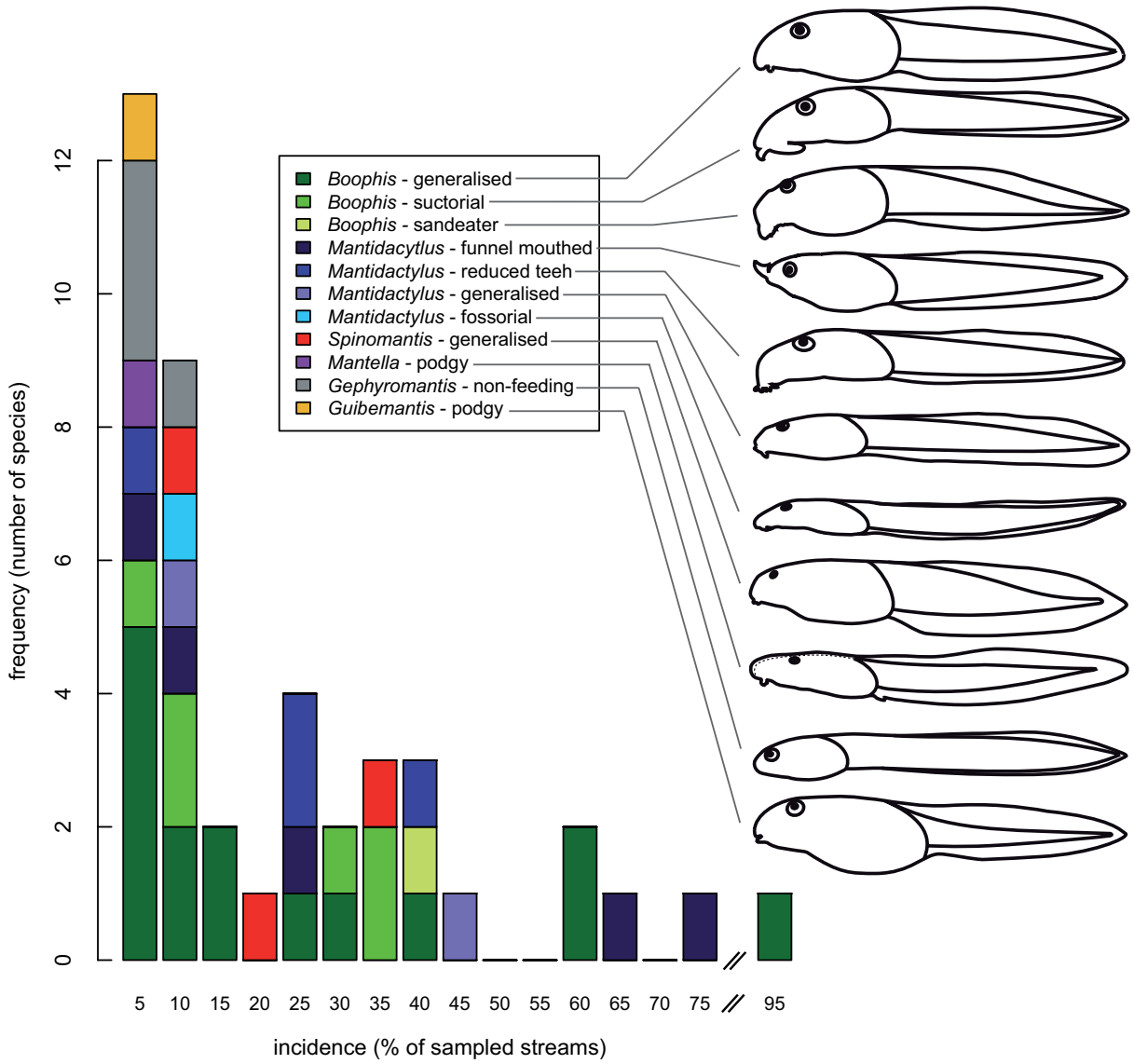


**Figure 1** Frequency of incidence values of tadpoles in Ranomafana National Park. Each data point is coloured according to its eco-morphological guild. Data are based on the 29 repeatedly sampled streams, averaged, and rounded to the next full number. Schematic representation of the guilds is also provided.

## Ecology of eco-morphological guilds

We assigned all tadpoles to predefined eco-morphological guilds based on a number of morphological key features (oral disc, body shape; see Table 3). Often, these eco-morphological guilds fit phylogenetic groups (usually subgenera) but there are also some exceptions. Most of the eco-morphological guilds can be found in the majority of streams, but most of them also include species that occur only in single streams. The incidence values of tadpoles were highly comparable for all species between 2007 and 2008 (Appendix Figure 1). None of the eco-morphological guilds consists of only wide spread species (Figure 1), however *Guibemantis* – podgy, *Gephyromantis* – non-feeding, *Mantella* – podgy, and *Mantidactylus* – fossorial can be considered to have a very restricted distribution as tadpoles in streams.

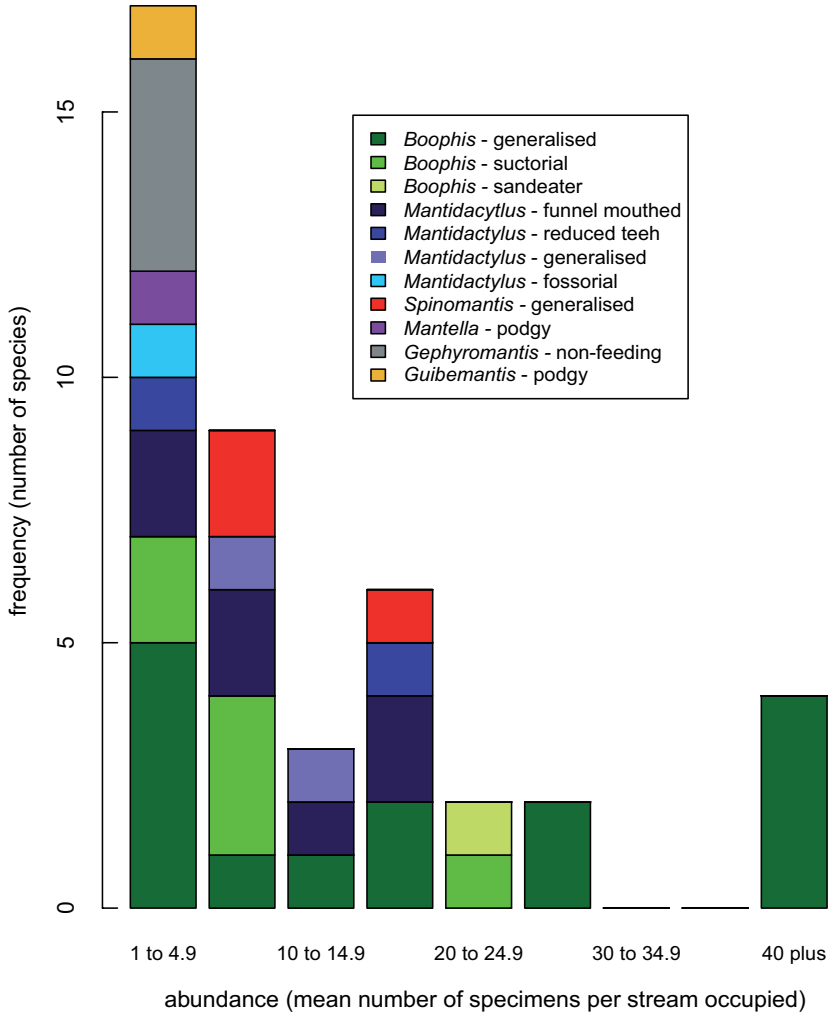


**Figure 2** Frequency of abundance values of tadpoles in Ranomafana National Park. Abundance data were grouped in steps of 5. Each data point is coloured according to its eco-morphological guild. Data are based on the 29 repeatedly sampled streams, and averaged.

The patterns of abundance (Figure 2) within the eco-morphological guilds differed from the patterns of incidence. Using the mean abundance of tadpoles in the streams occupied by a species, our data show that by far the most abundant tadpoles (20 or more specimens per site) belong to three eco-morphological guilds restricted to species of the genus *Boophis*. Ten out of the 11 eco-morphological guilds contain species with low abundances of 10 or less specimens per site, including all species of the four eco-morphological guilds with low incidence values. Assuming more than five specimens within a 30 m stream section as likely to be sampled, all but the four mentioned eco-morphological guilds are likely to be found if various streams are sampled. In contrast to incidence values, abundance data of several species differ substantially between years (Appendix Figure 2).

We graphically evaluated first the incidence (percentage of streams occupied, Figure 1) and second the abundance (mean number of specimens in streams occupied, Figure 2) of members of eco-morphological guilds. Species that occupy the majority of streams (> 50%, > 14 streams) can be found in the eco-morphological guild *Boophis* – generalised and in the Mantidactylus – funnel

mouthed tadpoles of the subgenus *Chonomantis* (Figure 1). These eco-morphological guilds, however, also include species that occur only in few or even a single stream. Seven out of the predefined 11 eco-morphological guilds were found in nine or more out of the 29 sampled streams, all belonging to the genera *Boophis*, *Mantidactylus* and *Spinomantis*. All eco-morphological guilds except "*Boophis* – sand eater" (i.e. *Boophis picturatus*) contained species occurring in the minority of streams (10% or less), including all the species of four eco-morphological guilds "*Mantidactylus* – fossorial" (*Hylobatrachus*; 1 species), "*Mantella* – podgy" (1 species), "Gephyromantis – non-feeding" (3 species), and "*Guibemantis* – podgy" (1 species).

## Species ecology

Species incidence and abundance is positively correlated (Figure 3); lme, $F_{1,42} = 29.30$, $p_{incidence} < 0.001$). This was consistent in both years of sampling as the variable "year" could be removed from the model as fixed factor. There are few exceptions such as *Boophis* sp. 42 (= *B.* sp. aff. *goudoti*; here labelled as Bosgo; for a list of abbreviations, see Table 3). Considering only the 22 most abundant species and therefore reducing the influence of the large number of very rare species led to slightly weaker but still significant results (lme, $F_{1,21} = 6.03$, $p_{incidence} = 0.023$). The three most omnipresent species (Figure 3: *Boophis* sp. 16, *B. reticulatus*, and *B. elenae* labelled as Bosbo, Boret, and Boele, respectively) all belong to the eco-morphological guild of "*Boophis* – generalised". Instead, *Mantidactylus* species with high incidence in general show relatively low abundances whereas the latter values may vary between years (Figure 3, for variation see Appendix Figure 2 (e.g. *M. melanopleura*)).

Incidence of tadpoles of anuran species in RNP is highly comparable between years (Appendix Figure 1) but mean abundance of a species in streams occupied by this species can vary strongly between years (Appendix Figure 2). This is especially true for some of the *Boophis* species, but also *Mantidactylus melanopleura*, the most common species from the funnel-mouthed subgenus *Chonomantis* (Figure 3, Appendix Figure 1) shows this variation in abundance.

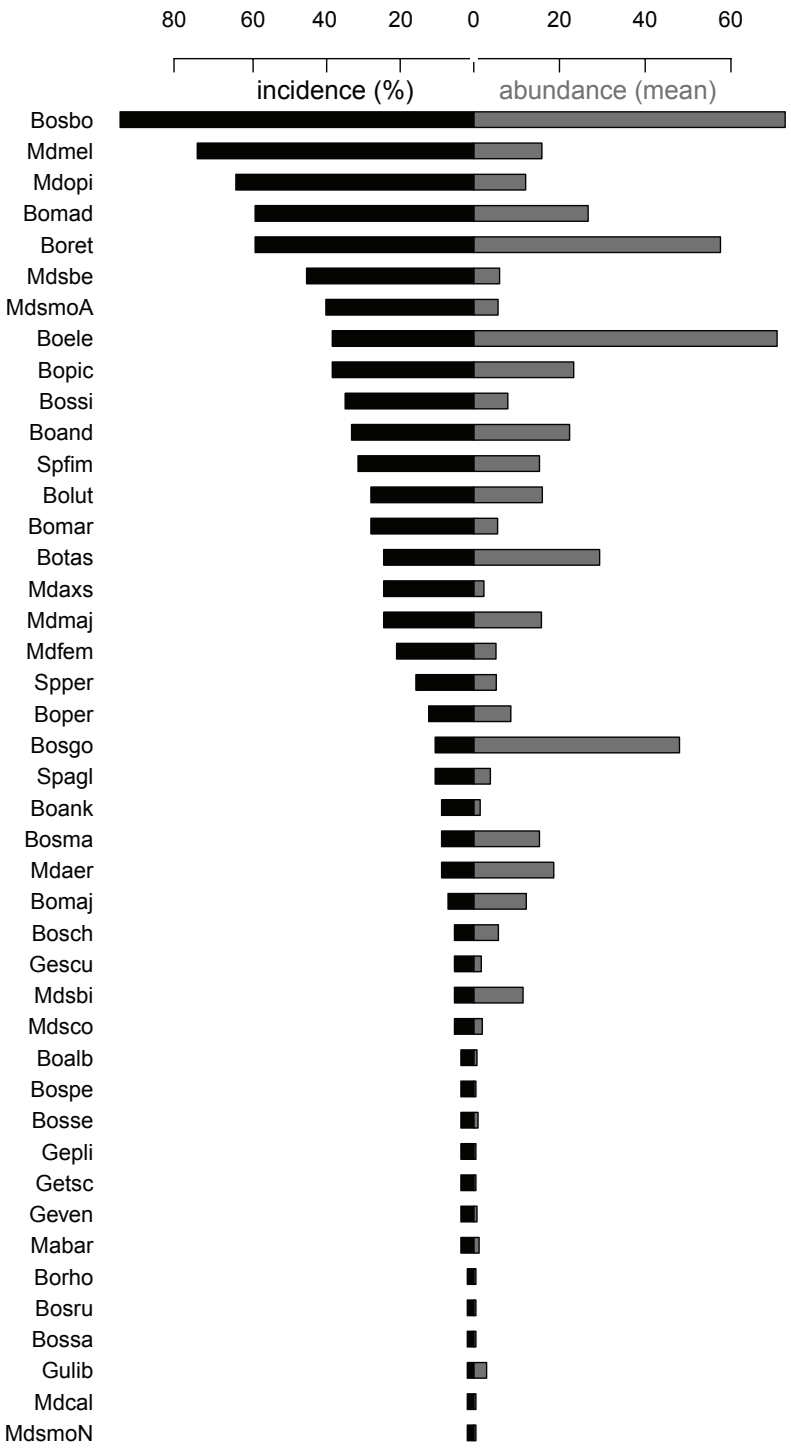


**Figure 3** Incidence (percentage of streams occupied) and abundance (mean number of specimens of a species in the streams occupied by this species) of all tadpole species found during repeated sampling of 29 streams in Ranomafana National Park (RNP) in wet seasons 2007 and 2008. Species are sorted according to their incidence. For a list of abbreviations used in this plot, see Table 3.

**Table 3** Species used for ecological analysis. Given are valid names (and names used in previous publications), the labels used for plots, references for tadpole descriptions and the sample size for the species that were included in multivariate analysis of breeding site choice (Redundancy Analysis, RDA; "n RDA") and microhabitat preferences (Principal Component Analysis, PCA; "n PCA"). n.s.d. = not sufficient data for respective analysis. References for tadpole descriptions are given as numbers, the full references are given in the appendix.

| Species | Label | Eco-morphological guild | Tadpole description | n RDA | n PCA |
|---|---|---|---|---|---|
| *Boophis albilabris* | Boalb | *Boophis* – generalised | 4, 10, 12 | n.s.d. | n.s.d. |
| *Boophis andohahela* | Boand | *Boophis* – suctorial | 16, in progress | 10 | 4 |
| *Boophis elenae* | Boele | *Boophis* – generalised | 7 | 12 | 9 |
| *Boophis luteus* | Bolut | *Boophis* – generalised | 2, 10 | 8 | 4 |
| *Boophis madagascariensis* | Bomad | *Boophis* – generalised | 2, 10 | 26 | 16 |
| *Boophis majori* | Bomaj | *Boophis* – generalised | 2, 15 | n.s.d. | 3 |
| *Boophis marojezensis* | Bomar | *Boophis* – suctorial | 10, in progress | 8 | 2 |
| *Boophis periegetes* | Boper | *Boophis* – generalised | in progress | n.s.d. | 1 |
| *Boophis picturatus* | Bopic | *Boophis* – sandeater | 1, in progress | 15 | 10 |
| *Boophis reticulatus* | Boret | *Boophis* – generalised | 10 | 20 | 14 |
| *Boophis rhodoscelis* | Borho | *Boophis* – generalised | 7 | n.s.d. | n.s.d. |
| *Boophis schuboeae* | Bosch | *Boophis* – suctorial | 5, in progress | n.s.d. | n.s.d. |
| *Boophis* sp. 8 = aff. *rufioculis* | Bosru | *Boophis* – generalised | in progress | n.s.d. | n.s.d. |
| *Boophis* sp. 13 = aff. *periegetes* | Bospe | *Boophis* – generalised | no | n.s.d. | n.s.d. |
| *Boophis* sp. 16 = aff. *boehmei* | Bosbo | *Boophis* – generalised | 13 | 31 | 27 |
| *Boophis* sp. 17 = aff. *sibilans* | Bossi | *Boophis* – suctorial | 7, in progress | 10 | 3 |
| *Boophis* sp. 18 | Boank | *Boophis* – suctorial | no | n.s.d. | n.s.d. |
| *Boophis* sp. 35 = aff. *majori* "long calls" | Bosma | *Boophis* – generalised | no | n.s.d. | 1 |
| *Boophis* sp. 37 = aff. *elenae* | Bosse | *Boophis* – generalised | in progress | n.s.d. | n.s.d. |
| *Boophis* sp. 38 = aff. *sambirano* | Bossa | *Boophis* – suctorial | in progress | n.s.d. | n.s.d. |
| *Boophis* sp. 42 = aff. *goudoti* | Bosgo | *Boophis* – generalised | no | n.s.d. | 1 |
| *Boophis tasymena* | Botas | *Boophis* – generalised | 10 | 9 | 4 |
| *Gephyromantis plicifer* | Gepli | *Ge.* – non-feeding | no | n.s.d. | n.s.d. |
| *Gephyromantis sculpturatus* | Gescu | *Ge.* – non-feeding | in progress | n.s.d. | n.s.d. |
| *Gephyromantis tschenki* | Getsc | *Ge.* – non-feeding | in progress | n.s.d. | n.s.d. |
| *Gephyromantis ventrimaculatus* | Geven | *Ge.* – non-feeding | in progress | n.s.d. | n.s.d. |
| *Guibemantis liber* | Gulib | *Gu.* – podgy | 17 | n.s.d. | n.s.d. |
| *Mantella baroni* | Mabar | *Mantella* – podgy | 8 | n.s.d. | n.s.d. |
| *Mantidactylus betsileanus* | Mdbet | *Md.* – generalised | 2, in progress | n.s.d. | n.s.d. |
| *Mantidactylus femoralis* | Mdfem | *Md.* – reduced teeth | 11 | 7 | 2 |
| *Mantidactylus majori* | Mdmaj | *Md.* – reduced teeth | 1, 11 | 11 | 7 |
| *Mantidactylus melanopleura* | Mdmel | *Md.* – funnel mouthed | 6 | 22 | 10 |
| *Mantidactylus opiparis* | Mdopi | *Md.* – funnel mouthed | 6 | 19 | 7 |
| *Mantidactylus* sp. 1 = *aerumnalis* | Mdaer | *Md.* – funnel mouthed | 6 | n.s.d. | 1 |
| *Mantidactylus* sp. 24 = aff. *biporus* "Ranomafana" | Mdsbi | *Md.* – generalised | 14, in progress | n.s.d. | 1 |
| *Mantidactylus* sp. 28 = aff. *betsileanus* "slow calls" | Mdsbe | *Md.* – generalised | in progress | 20 | 9 |
| *Mantidactylus* sp. 4 = cf *albofrenatus* | Mdcal | *Md.* – funnel mouthed | no | n.s.d. | n.s.d. |
| *Mantidactylus* sp. 47 = aff. *mocquardi* "Ambatolahy" | MdsmoA | *Md.* – reduced teeth | 11 | 16 | 2 |
| *Mantidactylus* sp. 48 = aff. *cowanii* | Mdsco | *Md.* – fossorial | 1 (as *lugubris*) | n.s.d. | n.s.d. |
| *Mantidactylus* sp. 59 | Mdaxs | *Md.* – funnel mouthed | 6 | n.s.d. | n.s.d. |
| *Mantidactylus* sp. aff. *mocquardi* "Namorona" | MdsmoN | *Md.* – reduced teeth | 11 | n.s.d. | n.s.d. |
| *Spinomantis aglavei* | Spagl | *Spinomantis* – generalised | 3, 18, in progr. | 7 | n.s.d. |
| *Spinomantis peraccae* | Spper | *Spinomantis* – generalised | 9, in progress | 9 | 4 |
| *Spinomantis* sp. 2 = *fimbriatus* | Spfim | *Spinomantis* – generalised | in progress | 9 | 3 |

**Stream characteristics influencing tadpole community composition**

Species composition of stream tadpole communities was highly correlated between the two sampling years (Mantel statistics $r = 0.701$, $p < 0.001$). We therefore assumed data of only 2008 as representative for analysis of species – habitat associations. We used only species with high incidence (present in at least seven out of the 32 streams) in 2008 to relate species presence or absence (and thus probably the choice of breeding sites by adults) to general stream characteristics and habitat variables of the surrounding forest. We found vast similarity in preferences within genera and within eco-morphological guilds (Figure 4). Except the "*Boophis* – sandeater" which forms its own eco-morphological guild, all *Boophis* group together and there also seems to be a conformity within the two eco-morphological guilds "*Boophis* – generalised" and "*Boophis* – suctorial". They can be found in wide streams without much vegetation cover (canopy cover, overhanging plants, and rather low slope). Sand eating *Boophis picturatus* (labelled Bopic) instead differs considerably from other *Boophis* species. This species avoids sites that are characterised by steepness, both of the forest floor and the stream. Whereas the size of the stream (width & depth) seems to be less of importance, the presence of this species is positively associated with leaf litter in the forest. The same is true for two of the "*Spinomantis* – generalised" species, which cluster very close to *B. picturatus*. The third *Spinomantis* species, *S. fimbriatus* (labelled Spfim) differs not only from the first two members of this genus; indeed it seems to differ from all other species in habitat choice. It is found in smaller and steeper streams at sites with more cover. *Mantidactylus opiparis* (labelled Mdopi), one of the two "*Mantidactylus* – funnel mouthed" species included in this analysis, shows a breeding site choice comparable to *Spinomantis fimbriatus* but with even stronger habitat specificity. In contrast, the second of the common "*Mantidactylus* – funnel mouthed" species, *M. melanopleura* (labelled Mdmel) differs considerably from *M. opiparis* showing a breeding site choice more similar to the two other *Spinomantis* species. From the "*Mantidactylus* – reduced teeth" (*Ochthomantis*) species we included three in this analysis which all show a similar habitat choice, similar to "*Boophis* – generalised" (larger streams, low slope). In general, characteristics of the terrestrial habitat seem to exert weaker influences on the presence or absence of species than the stream habitat variables, a phenomenon that we will analyse more in detail elsewhere.

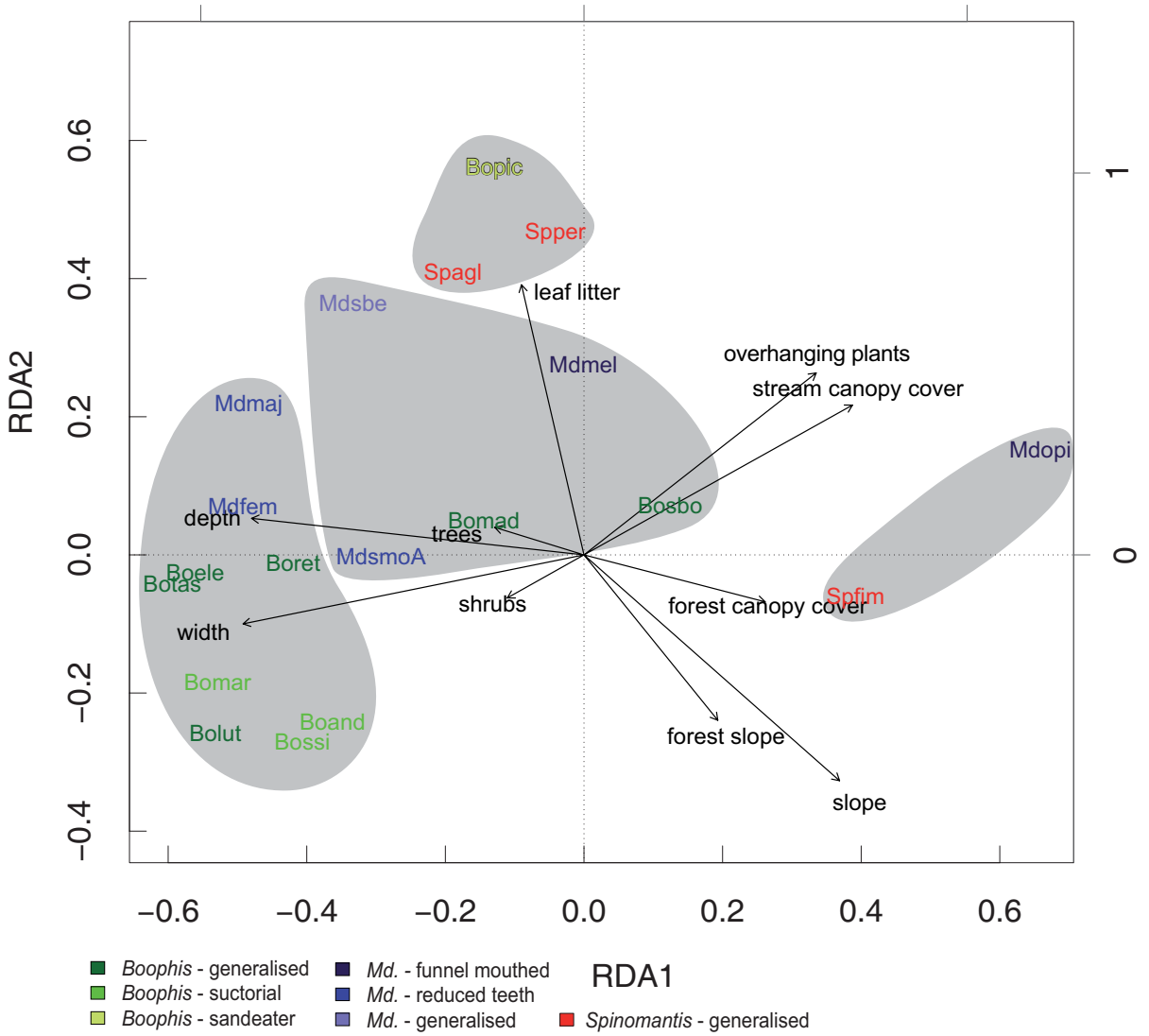


**Figure 4** Habitat choice of frogs from Ranomafana National Park (tadpole incidence). A Redundancy Analysis (RDA) was performed on a site-species matrix and a site-habitat matrix, an RDA plot is displayed. Species labels are coloured according to their eco-morphological guild. Data were used from 33 streams sampled in 2008 but only including species that occurred in seven or more streams. For a list of abbreviations used as labels in this plot, and the sample size for the different species, see Table 3. For a better visual interpretation, species are plotted as labels despite the fact that they are linear combinations and should be represented by arrows. Angles between species, between habitat variables, and between species and habitat variables can be interpreted as correlations (Zuur et al., 2007). Species that appear close to the origin, such as the two "*Boophis* – generalised", can not well assigned to habitat variables as they occur in almost all streams and therefore with almost all habitat variables. As additional information, species that in fact co-occur in streams (irrespective of any habitat variables) are marked by grey background shading (as retrieved from cluster analysis; for original results also displaying different numbers of clusters see Appendix Figure 3).

### Co-occurrence of species

To further evaluate the co-occurrence of species irrespective of their preferences for breeding site habitat characteristics, we performed a cluster analysis. Species clusters fit their grouping by habitat preferences and usually consist of members of different eco-morphological guilds (Figure 4, grey shaded). Further information, including alternative numbers of clusters, are given in Appendix Figure 3.

### Microhabitat choice

The pattern of microhabitat choice within streams was characterised by similarities within and differences between different eco-morphological guilds (Figure 5). Preferences for all microhabitats in fast flowing stream sections and the stony parts of slow flowing stream sections were highly correlated. Species that prefer one of the "fast flowing" microhabitats, in general also prefer one or more of the other "fast flowing"-microhabitats, as well as "slow rock" and "slow gravel". These microhabitat preferences therefore are well represented (negative) in the first PC (explaining 38.7% of the variance). This is especially true for species that have high (negative) values on this axis, such as the three members of "*Boophis* – suctorial". Some of the "*Boophis* – generalised" show the same trend. Species also placed on this axis but closer to the origin may show a similar but more specific preference and are therefore not well represented by PC1. *Boophis picturatus* (labelled Bopic; "*Boophis* – sandeater"), for instance, was shown before to have a preference for "fast sand"-like microhabitat (Altig & McDiarmid, 2006) but not to other substrates. Its value for PC1 is therefore closer to zero. The majority of *Mantidactylus* species have positive values on PC1, i.e., they avoid the microhabitats mentioned before. Good examples are the three "*Mantidactylus* – reduced teeth" (*Ochthomantis*) species that are placed close to each other. Several species are also distributed along the PC2 axis (explaining 12.4% of variance). This axis mainly represents preferences for "slow sand" (negative) and "slow leaves" (positive). The three "*Mantidactylus* – funnel mouthed" (*Chonomantis*) species included in this analysis are all positively correlated to PC2 but differ in their values along the PC1 gradient. Based on these and previous results (Grosjean et al., in press), it appears that for all *Chonomantis*, the "leaves" substrate is important (leaves is represented in both axes) but they differ in their preferences for slow or fast running parts. It needs to be noted, however, that the number of streams that we used to calculate the preference values differs between species (see methods section and Table 3). For three of the "*Boophis* – generalised" members that are placed separately from the other "*Boophis* – generalised" (*Boophis periegetes*, *B.* sp. 35, *B.* sp. 42 labelled as Boper, Bosma, and

Bosgo, respectively), data of only a single stream were available. For sample size of species, see Table 3.

### Stream vs. microhabitat choice

We found no pattern comparing general habitat choice (habitat characteristics influencing the presence or absence of species in streams) and tadpole microhabitat preferences (Mantel test, Mantel $r = -0.98$, $p = 0.80$). Species that select similar streams for reproduction thus do not have similar or explicitly different microhabitat preferences in the tadpole stage.

## Discussion

### Incidence and abundance of tadpoles

Streams play a major role for anuran reproduction in Madagascar's rainforests. Almost half of all frogs of RNP reproduce in forest streams and thereby form the world richest stream tadpole communities (Strauß et al., 2010). As we analysed in detail in the present study, we detected 42% of all frogs and 54% of all Mantellidae known from the studied part of RNP (including our new discoveries) by sampling tadpoles exclusively in streams. This represents about 45% of tree frogs and 79% of leaf litter plus riparian frogs, 55% and 79% if considering only mantellids (see Table 2).

These values are high compared with some other tropical regions. In Neotropical terra-firme forest, Gascon (1991) and Magnusson and Hero (1991) found only about 13% and 8% of the local species pool breeding in streams, respectively. In Borneo instead, the proportion of stream breeders is similar to that in Madagascar (Zimmerman & Simberloff, 1996). This might be caused by several reasons. Firstly, due to topography of Madagascar there is only little availability of lentic water bodies which might limit the number of pond breeding species able to co-exist, while in the Neotropical study areas a high number of ponds is available. Secondly, due to the virtual absence of fish in tributary streams in RNP an important tadpole predator is missing. Thirdly, beside environmental traits, historical colonisation events and phylogenetic constraints restrict species in their habitat use at this spatial scale (pond vs. stream, Cadle & Greene, 1993; Zimmerman & Simberloff, 1996). In Borneo a high proportion of stream breeders occur although many ponds are available (Zimmerman & Simberloff, 1996).

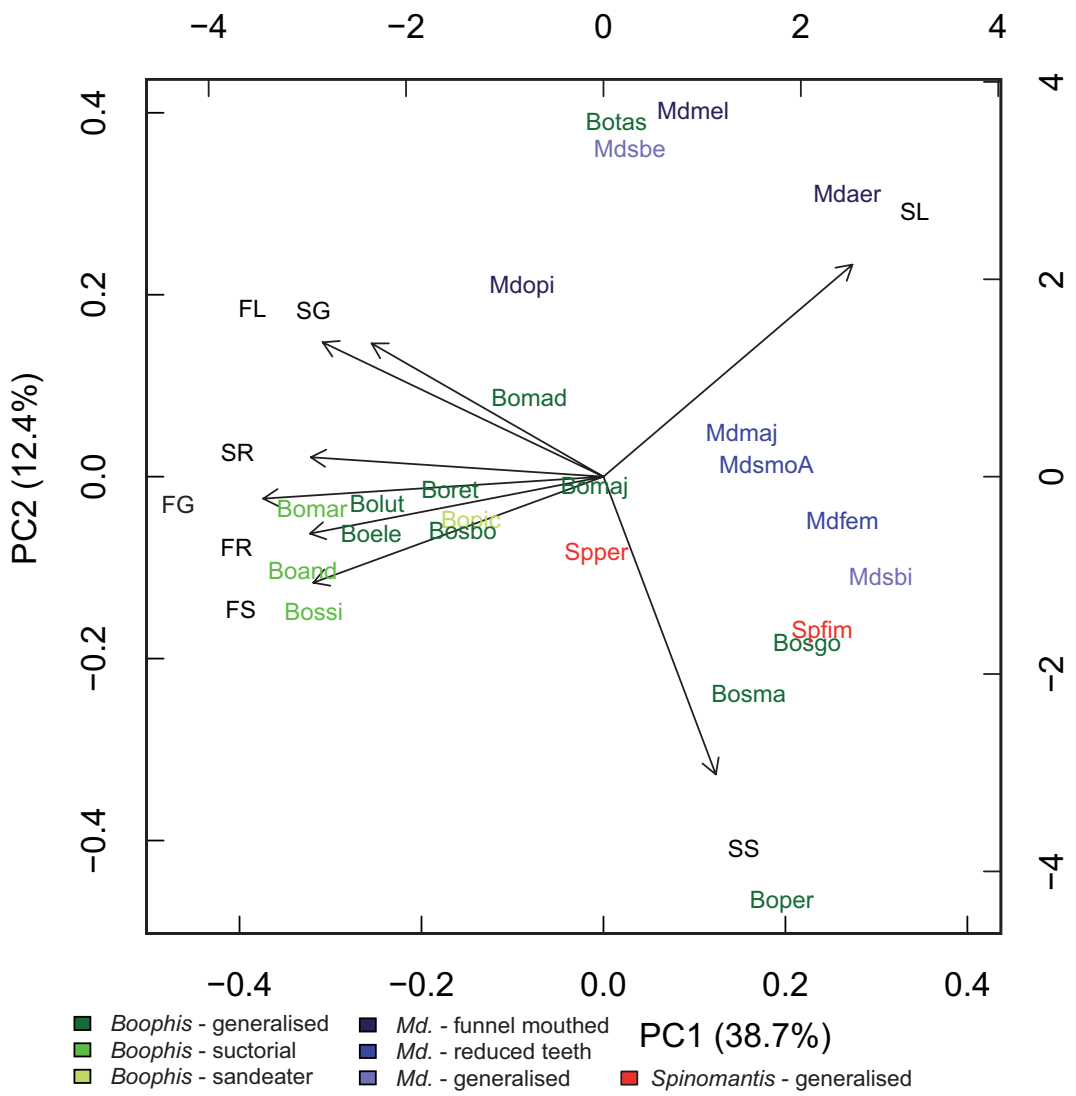


**Figure 5** Microhabitat preferences of tadpoles from Ranomafana National Park within streams. For each species, a preference index (Ivlev, 1961) for each of the eight microhabitats was calculated. Microhabitat preference values were summarised using Principal Component Analysis. The vectors show the preferences for microhabitat variables. Additionally, species labels are plotted according to their scores and coloured according to their eco-morphological guild. Data were used only from streams where the respective species appeared with at least eight specimens. Data are from 33 streams sampled in 2008. For a list of abbreviations used as labels in this plot, and the sample size for the different species, see Table 3.

Among tadpoles in RNP streams we observed a strong gradient from widespread to localised species (high incidence vs. low incidence). The widespread species in general also show high abundances, but their abundances were found to vary considerably between years. Widespread species (found in > 50% of the streams) belong to a generalised eco-morphological guild (i.e., "*Boophis* – generalised") as well as to a highly derived guild (i.e., funnel mouthed *Chonomantis*) although species in these two guilds do not share the same preferences for streams and

microhabitats. A range of four additional eco-morphological guilds contain relatively common species which live in 30% and more of the streams. These include one generalised species ("*Mantidactylus* – generalised" guild), one species probably adapted to strong currents ("*Boophis* – suctorial"), and two guilds with reduced oral structures ("*Mantidactylus* – reduced teeth" and "*Boophis* – sandeater" guilds). Hence, widespread species occur throughout specialized and generalised guilds, and there is no tendency of guilds of more generalised morphology to have a higher incidence in streams. On the contrary, all species with high abundances belong to a generalised eco-morphological guild ("*Boophis* – generalised"). Whether this is due to (1) a larger number of reproducing individuals of these species, (2) a larger clutch size, or (3) a bias in detectability of tadpoles cannot be conclusively assessed at present. However, according to our own unpublished observations, at least two of the four species with highest abundances (*Boophis* sp. 16 and *B. reticulatus*) are unlikely to have particularly large clutch sizes. We furthermore are convinced that, maybe except for some very specialized guilds (e.g., "*Mantidactylus* – fossorial"), capture probability of tadpoles was comparable across species and guilds.

"*Mantidactylus* – fossorial" tadpoles were among the rarest species encountered in our samples although adults were often observed sitting on rocks at the river banks. The tadpole of the single species of this guild in the streams studied (*Mantidactylus* sp. aff. *cowanii*; described as tadpole of *M. lugubris* by Altig & McDiarmid (2006)) has an elongated appearance, a flattened body, extremely reduced tail fins, keratodonts that are transformed into a bow-net like structure and a black-reddish colouration. These features have been observed for a range of fossorial stream-dwelling anuran larvae (see Wells, 2007) causing our naming of this guild. Altig and McDiarmid (2006) state that this tadpole did not attempt to burrow when kept in a plastic container with sand. According to our observations from another tadpoles surveys, these tadpoles can also be found in leaf litter agglomerations in deep parts of the streams, and they might thus in general be restricted either to specific parts of the streams or difficult to sample, e.g. due to fossorial life.

The low incidence values of some species, which were observed for members of almost all eco-morphological guilds, can be explained by different factors: some species might in fact be at the edge of their altitudinal or latitudinal distribution at RNP and were therefore missing from many streams. This could be the case for few species such as *Boophis* sp. aff. *rufioculis* (*Boophis* sp. 8), which we found only during 2008 sampling in three (including two of the additionally sampled) streams located close to each other and at the border of our sampling area, and which is very common in other areas such as Imaitso forest near Andringitra National Park that are located at higher elevations than our study area. Other species are pond breeders that either accidentally

reproduce in streams or choose the few very slow moving streams, such as *Guibemantis liber* (Vejarano et al., 2006). A similar case may apply to all "*Gephyromantis* – non-feeding" species included in this study. Due to the combination of their rareness and the fact that they seem to be non-feeding tadpoles (Randrianiaina et al., unpublished), eggs may actually be placed outside the stream to form a jelly nest and tadpoles later be washed in streams by accident. Many of the rare species, however, are clearly stream-dwelling tadpoles and are found across the study area and their low incidence values may reflect true rareness.

Tadpoles in RNP are not randomly distributed between streams. Mantel test showed that communities found in comparable habitat (characteristics of stream and surrounding forest) are very similar in species composition. This differs from the findings of Gascon (1991) who states for tropical temporary ponds that the occurrence of single species is related to habitat characteristics, but there are no habitat driven distinct communities on a local scale. Beside the fact that we here studied stream communities, the high species richness of the communities in RNP might be an important key to reveal environmental filters that might be overseen in less species rich communities (Strauß et al., 2010).

Tadpole community composition in RNP is highly comparable between years. This agrees with results for adult frog communities in South-East Asia and the Neotropics (Inger et al., 1986; Zimmerman & Simberloff, 1996) that were interpreted as being caused by constant habitat conditions and therefore constant adult populations (Inger et al., 1986). Furthermore, in tropical rainforests frog home ranges may be very small (Inger et al., 1986) and migration is only of minor importance (De Oliveira & Eterovick, 2010) but no such data on adults exist from Madagascar.

### Species habitat associations

We found the general trend that most species prefer streams that are wide, deep, and not steep. This corresponds to data from RNP from 2007 (Strauß et al., 2010) and to the results of Eterovick & Barrata (2006) who showed that shallow habitats with strong current are avoided by most species. Whereas tadpole community species richness is mainly determined by stream characteristic (size, velocity, see Strauß et al., 2010) the occurrence of some species can also depend on forest habitat characteristics, such as forest leaf litter depth.

However, habitat use is a matter of scale and whereas adults choose breeding sites (Inger et al., 1986; Alford, 1999; Afonso & Eterovick, 2007b; Magnusson & Hero, 1991), tadpoles choose microhabitat. Differences and similarities of species regarding breeding site choice are not correlated to the ones of microhabitat choice. This is a clear indication that the assembling of natural stream tadpole communities is probably not influenced by competition (Inger et al., 1986; Eterovick & Barata, 2006; Strauß et al., 2010). The independence of habitat preferences at both

scales is also supported by examples for contradictory choices. Such an example are suctorial tadpoles ("*Boophis* – suctorial" eco-morphological guild) that, as most other species, are found in large streams with low slope, but within the streams they choose their microhabitat in the faster running sections.

In other studies, phylogenetic history has been identified as a determinant of habitat preferences that can influence, for example, whether adults choose ponds or streams for reproduction (Zimmerman & Simberloff, 1996). Here we found some similarities within eco-morphological tadpole guilds regarding the incidence of species in the streams studied (and thus breeding site choice of adults), and the guilds partially have a phylogenetic background (they generally fit Mantellidae phylogeny as given by Glaw & Vences, 2006). However, also species that have very similar tadpoles but belong to different taxonomic species groups (e.g., members of "*Boophis* – suctorial") show very similar breeding site preferences. This indicates that eco-morphological adaptations can overlay the phylogenetic background.

On a tadpole-microhabitat scale microhabitat choice has previously been found to lack a phylogenetic signal (Eterovick et al., 2010) but to be influenced by morphological adaptations and feeding ecology (Inger et al., 1986). Our data are in agreement with these previous results because some eco-morphological guilds species are conspicuously similar in microhabitat preferences, whether the guilds totally correspond to phylogenetic clades ("*Mantidactylus* – reduced teeth" and "*Mantidactylus* – funnel mouthed") or not ("*Boophis* – suctorial").

The *a priori* sorting of Madagascan tadpoles into eco-morphological guilds as applied in this study was based on only two general morphological parameters, body shape and oral disc modification. Our data confirm that these guilds in fact correspond to distinct ecologies and thus validate the approach of defining eco-morphological guilds based on morphology alone, even for species for which no ecological data are available (Altig & Johnston, 1989).

Summarising, streams represent the most important breeding habitat for anurans in Madagascar's rainforest. Eco-morphological guilds can show a species specific distribution and within streams, but patterns on both spatial scales are not correlated. The very species rich communities usually consist of several eco-morphological guilds of which some are found in almost all communities. Within the communities, eco-morphological guilds are often separated by habitat partitioning, which is mainly determined by morphological constraints. There is no evidence for competition as shaping force in tadpole communities.

## Authors' contributions

AS participated in the design of the field study, conducted field work, designed and conducted statistical analyses, and drafted the manuscript. RDR conducted fieldwork and contributed morphological data to prove molecular findings. MV participated in the design of the field study and analysis and significantly developed the draft. JG designed the field study, conducted fieldwork, and significantly developed the draft.

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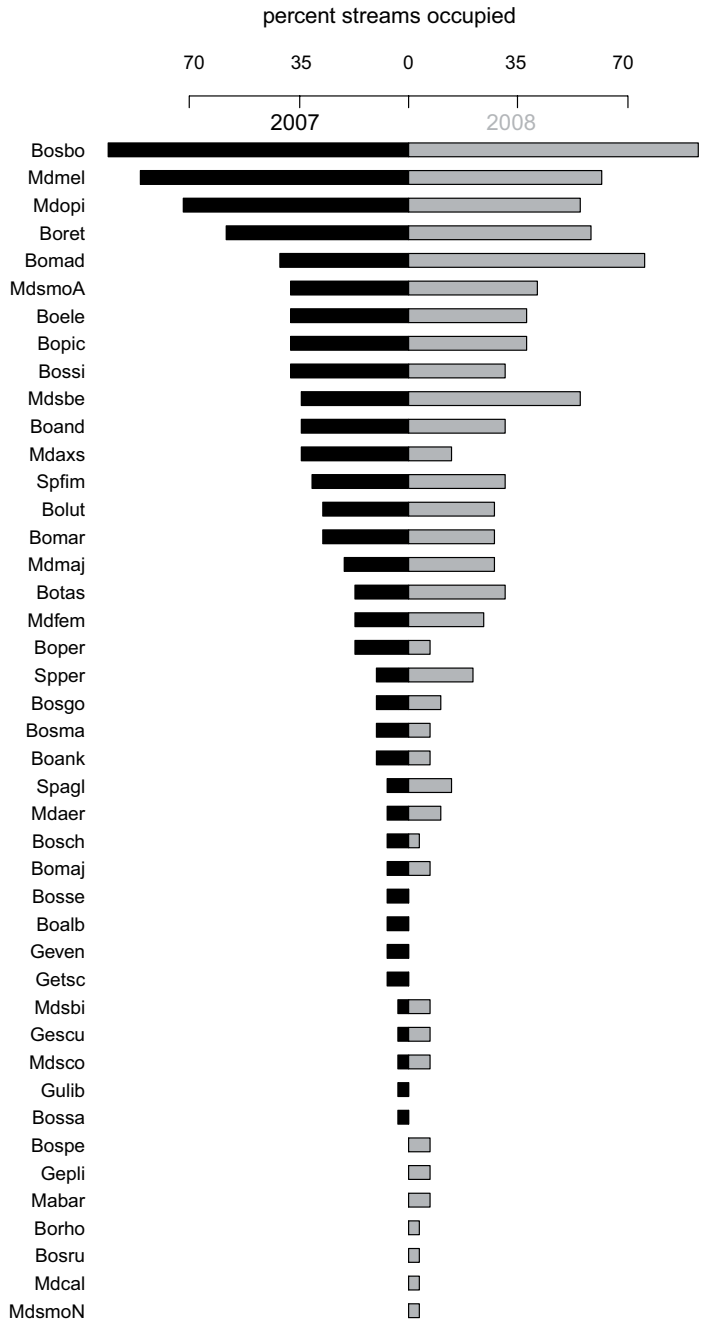
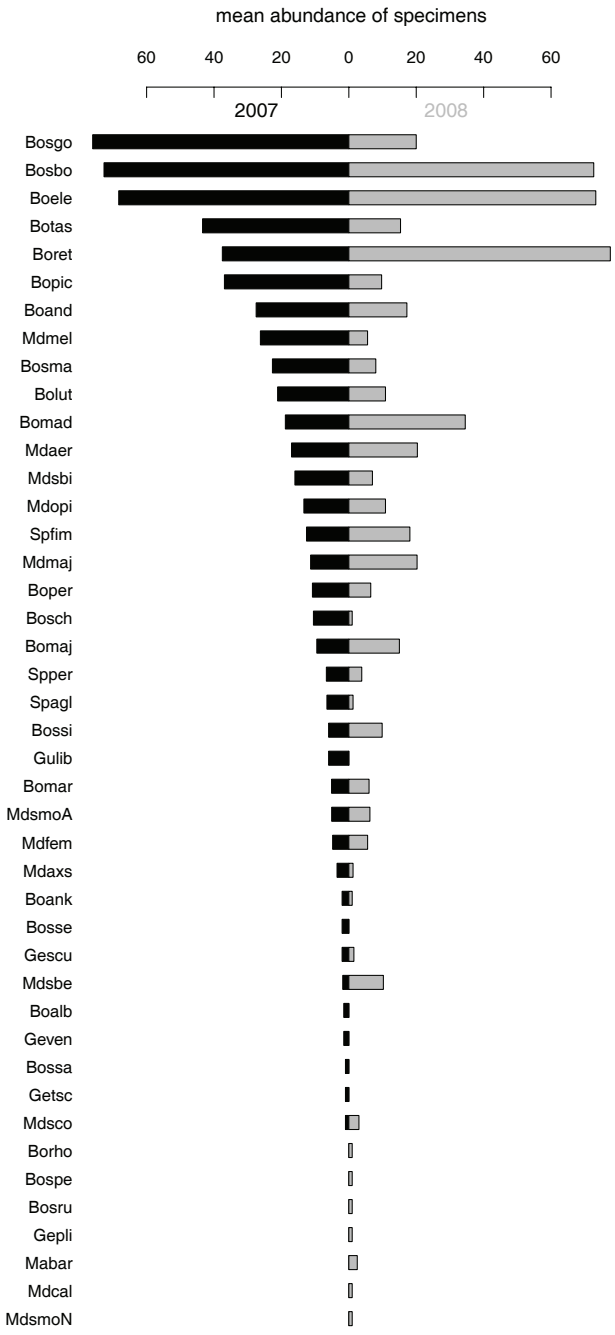
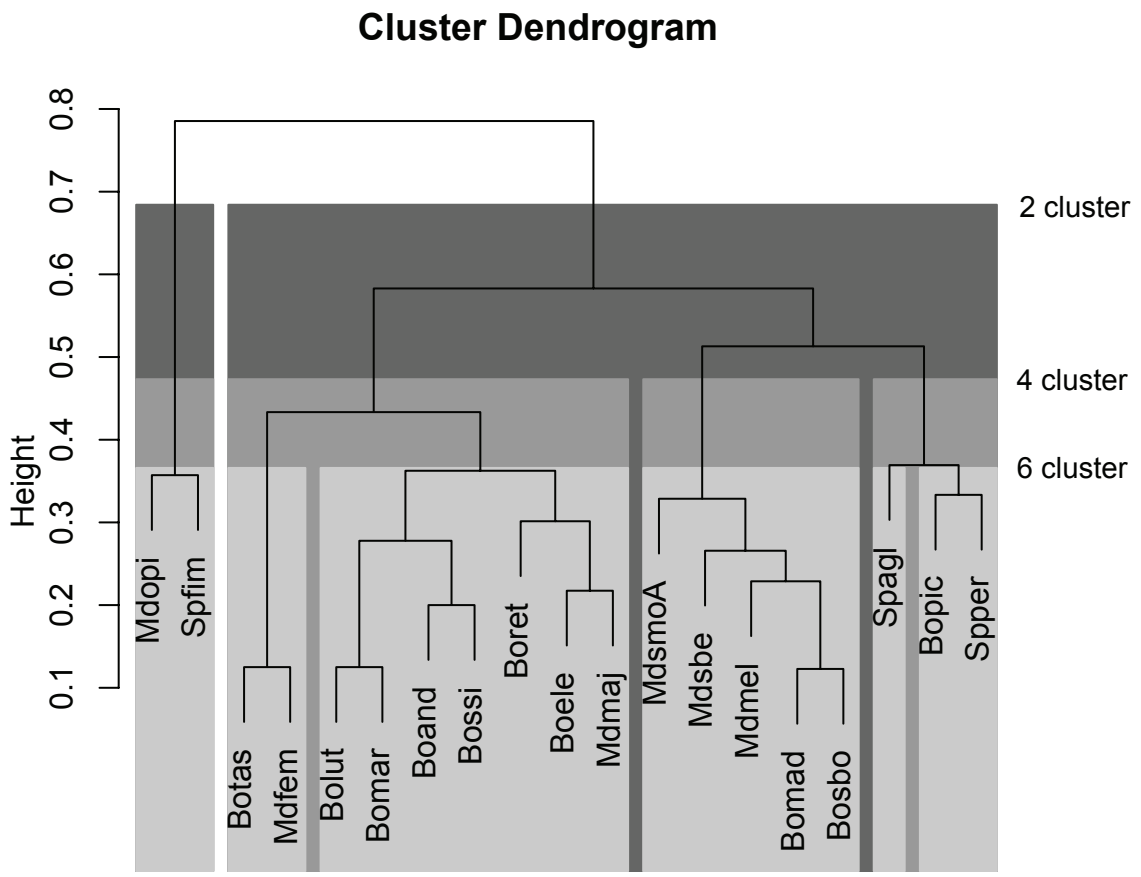
# Appendix




**Appendix Figure 1** Incidence values for all species of tadpoles found in the wet seasons 2007 and 2008 in Ranomafana National Park. Data are based on 29 streams that we sampled repeatedly, species are sorted according to their incidence in 2007. For a list of abbreviations used as labels in this plot, see Table 3.




**Appendix Figure 2** Abundance of all species of tadpoles sampled in the wet seasons 2007 and 2008 in Ranomafana National Park. Data are based on 29 streams that we sampled repeatedly, species are sorted according to their abundance in 2007. For a list of abbreviations used as labels in this plot, see Table 3.




**Appendix Figure 3** Cluster dendrogramm showing co-occurrence of tadpoles based on incidence data of the 19 species that were sampled in at least 7 streams in Ranomafana National Park. Grey background boxes indicate clusters, from dark to light grey showing 2, 4, and 6 cluster. For a list of abbreviations used as labels in this plot, see Table 3.

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# The world's richest tadpole communities show functional redundancy and low functional diversity: ecological data on Madagascar's stream-dwelling amphibian larvae

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# Abstract

Functional diversity illustrates the range of ecological functions in a community. It allows revealing the appearance of functional redundancy in communities and processes of community assembly. Functional redundancy illustrates the overlap in ecological functions of community members which may be an indicator of community resilience. We evaluated patterns of species richness, functional diversity and functional redundancy on tadpole communities in rainforest streams in Madagascar. This habitat harbours the world's most species-rich stream tadpole communities which are due to their occurrence in primary habitat of particular interest for functional diversity studies.

Species richness of tadpole communities is largely determined by characteristics of the larval habitat (stream structure), not by adult habitat (forest structure). Species richness is positively correlated with a size-velocity gradient of the streams, i.e. communities follow a classical species-area relationship. While widely observed for other taxa, this is an unusual pattern for anuran larvae which usually is expected to be hump-shaped. Along the species richness gradient, we quantified functional diversity of all communities considering the similarity and dissimilarity of species in 18 traits related to habitat use and foraging. Especially species-rich communities were characterised by an overlap of species function, i.e. by functional redundancy. By comparing the functional diversity of the observed communities with functional diversity of random assemblages, we found no differences at low species richness level, whereas observed species-rich communities have lower functional diversity than respective random assemblages.

We found functional redundancy being a feature of communities also in primary habitat, what has not been shown before using such a continuous measure. The observed species richness dependent pattern of low functional diversity indicates that communities with low species richness accumulate functional traits randomly, whereas species in species-rich communities are more similar to each other than predicted by random assemblages and therefore exhibit an accumulation of stream-specific functional traits. Beyond a certain species richness level, therefore, stream-specific environmental filters exert influence whereas interspecific competition between species does not influence trait assemblage at any species richness level.

Keywords: tadpoles; functional diversity, redundancy, species richness, tropics, Madagascar

# Background

Diversity is an important characteristic of communities, with paramount influences on ecosystem properties (Tilman, 1999). A wide range of measures have been applied for quantifying diversity, the simplest of which is species richness (SR): the number of species in a community (Magurran, 2007). SR assumes species as comparable, distinct entities of similar ecological importance. However, differences between species regarding ecological traits may range from almost ecologically similar to very different. Therefore, in recent years the focus has turned from SR towards functional diversity, which considers components that influence ecosystem function rather than taxonomic units (Tilman, 2001). The general concept of species function being more important than species richness has been shown in several studies, e.g. in predicting plant community resistance (Joshi et al., 2000) and plant biomass accumulation (Tilman et al., 1997).

A common approach in measuring functional diversity is classification of functional species groups (Naeem & Li, 1997; Tilman, 2001; Tilman et al., 2001). This requires an *a priori* classification of species resulting in a discontinuous and, therefore, less accurate measure of functional diversity (Petchey et al., 2004) than a continuous measure (FD) defined by Petchey & Gaston (2002b, 2006). Additionally, it can be difficult to fit species varying ecomorphologically in a complex multidimensional space into predefined groups defined by a limited number of characters (e.g. Randrianiaina et al., 2009). Alternatively, FD compiles a variable range of ecological characteristics of species and is regarded as a very powerful measure of functional diversity (Petchey & Gaston, 2007).

Patterns between changes in functional diversity and SR provide information on the relative contribution of a species' ecological function to the sum of ecological functions of the community. Therefore, if functional diversity and SR show a one by one relationship, all species are different and contribute equally. Deviations from this pattern occur with differences in species contribution, e.g., if SR changes but functional diversity remains constant, the additional or diminished species do not exhibit unique ecological traits and can be considered as functional redundant (Walker, 1992). Patterns of functional redundancy were identified using FD in mammal, bird (Flynn et al., 2009), and amphibian communities (Ernst et al., 2006; Ernst et al., 2007). However, these findings of functional redundancy are so far only related to anthropogenically disturbed landscapes. Comparing FD of observed and random assemblages can be used to test for non-randomness, which can highlight general processes of community assembly (Holdaway & Sparrow, 2006), such as competition or environmental filtering (Petchey et al., 2007). Communities harbouring a large number of species are likely to contain species that are redundant in their ecological traits. The question of functional diversity and redundancy in

species communities is therefore of particular interest when facing taxonomic groups that are rich in species. Tropical anuran communities represent an appropriate model as they are known to be remarkably rich but still taxonomically ascertainable. Studies on tropical frogs often focus on the ecology of adults (Parris & McCarthy, 1999; Vallan, 2000; Parris, 2004; Afonso & Eterovick, 2007; Ernst & Rödel, 2008), and have shown that SR can be predicted by environmental variables (Parris, 2004; Keller et al., 2008), and that species specific habitat requirements may be overlaid by stochastic processes (Ernst & Rödel, 2005, 2008). Minor attention has focused on functional diversity and functional redundancy in tropical amphibians, although Ernst et al. (2006; 2007) showed that functional redundancy can be found in disturbed tropical frog communities and the classical measure of species richness fails to reflect the real dimensions of biodiversity.

Of the available amphibian community studies, only a few included larval stages (Inger & Voris, 1993; Eterovick, 2003; Kopp & Eterovick, 2006). Even less attention was given to diversity patterns of the tadpole communities themselves (Eterovick & Wilson Fernandes, 2001; Eterovick & Barros, 2003), although in pioneering studies different habitat variables were found to be possibly related to SR of tadpole communities (Eterovick, 2003; Afonso & Eterovick, 2007). There are no published data on functional diversity in tadpole communities and the validity of SR as an adequate measure of diversity remains to be verified.

This is especially true as there are several ways tadpole communities might influence ecosystem function. There is evidence that e.g. by moving sediment and feeding on primary algae producers, tadpoles can alter algae abundance, composition, and chlorophyll *a* level and therefore net primary production in stream ecosystems (Connelly et al., 2008). Furthermore, due to their influence on basal resources e.g. removing sediments and exposing periphyton, they affect other primary consumers (Ranvestel et al., 2004). Tadpoles can therefore affect stream ecosystem structure and function (Ranvestel et al., 2004; Connelly et al., 2008) depending on where they live in the stream and how they forage. This might be especially true if some higher trophic levels are missing in the ecosystem.

The remarkable backlog of tadpole community studies may have been caused by identification difficulties, especially in species-rich tropical communities where the ecological importance of tadpole communities may be paramount (Kupferberg, 1997; Flecker et al., 1999; Ranvestel et al., 2004; Whiles et al., 2006). Madagascar, regarded to be one of the most important hotspots for biodiversity conservation (Myers et al., 2000) harbours over 400 fully endemic frog species (Glaw & Vences, 2007; Vieites et al., 2009). Even if many of these species are yet undescribed scientifically, a near-complete database of genetic markers exists (Vieites et al., 2009). This allows application of molecular identification methods to identify tadpoles to species (Vences et al.,

2005), and allows community studies of tadpoles in an area known to harbour rich frog communities (Glaw & Vences, 2007; Vences et al., 2008).

Here, we report on the SR and functional diversity of stream communities of tadpoles in Ranomafana National Park (RNP) in eastern Madagascar as determined by DNA barcoding, and on the environmental variables that might influence these measures of diversity. We addressed three main questions: (1) are stream tadpole communities in Madagascar as rich as expected given the highly diverse amphibian communities, (2) is SR predictable by either adult or tadpole related environmental variables, and (3) does the functional diversity measure expose patterns of diversity that are not detectable by SR and point to general rules of species' trait assemblage?

# Methods

### Study sites

We conducted fieldwork during the rainy season, February and March, 2007, in one of the centres of amphibian species richness in Madagascar, the Ranomafana National Park (RNP; 21°16'S; 47°25'E; 500 – 1500 m a.s.l.). RNP covers over 40,000 ha of mid-elevational rain forest and harbours over 100 frog species (Vieites et al., 2009). Due to varied topography and high average annual rain fall of 2,000 mm, RNP has numerous streams which are generally permanent, with broad variations in abiotic and biotic characteristics.

Study sites were represented by 30 m sections of 29 permanent streams without direct upstream link between any two sites and comprised various types of streams in a similar number. Streams of obvious different habitat characteristics were sampled alternately to avoid a time effect on sampling results for specific stream types. Of each 30 m section, three groups of habitat variables were recorded: (1) characteristics of the stream, representing habitat relevant for tadpoles, (2) characteristics of the adjacent forest, representing habitat relevant for frogs, and (3) structure of riparian vegetation, which is relevant for breeding activities.

*Aquatic habitat* – We laid transects consisting of adjoining 1×1 m quadrates crossing the stream perpendicularly. Starting at the downstream end of the sampling section, we recorded stream variables of 10 diagonal transects at intervals of 2 m, thus covering 33 % of the area of the sampling section. We recorded stream width (m) in the centre of each of these transversal transects, and averaged (variable *width*). Stream velocity was analysed by measuring the stream *slope* (m), i.e. the difference in altitude between the upstream and the downstream end of the 30 m stream section. We recorded in each 1×1 m quadrate the *canopy cover* (coded as 0 = absent and 1 = present, and averaged), and the proportion of each microhabitat type (%). We defined

microhabitat types based on ground substrate: *leaves* (organic material), *sand* (very finely grained up to ~3 mm grain size), *gravel* (grain size 3 mm to 25 cm), and *rock* (> 25 cm). As biotic habitat variables, we sampled *dragonfly* (Anisoptera) and *mayfly* (Ephemeroptera) *larvae* which we conserved in 99 % ethanol immediately in the field to avoid possible predation events within the sampling containers.

*Terrestrial habitat* – We recorded forest habitat characteristics on four circular plots of 6 m in diameter, equally distributed along the stream and their midpoint being in a distance of 7 m to the stream edge. These variables were the number of *SHRUBS* (≤ 5 cm stem diameter at eye level) and the number of *TREES* (> 5 cm), *CANOPY COVER* (%; estimated), and *LEAF LITTER* depth (cm; measured at 4×4 points and averaged). To measure riparian structural complexity, we took four photographs of the riparian vegetation of the stream, equally distributed along the 30 m of the stream section and alternating on the left and right side of the stream. The photographs covered an area of 3×2.25 m, with the bottom of each picture at the level of the water surface. *RIPARIAN VEGETATION* was then evaluated by projecting eight vertical and six horizontal grid lines onto the photograph, and measured by the number of tree structures such as branches and leaves at cross points of the grid lines.

### Species sampling, identification, and traits

We sampled tadpoles and invertebrates using dip nets of different sizes and materials, adjusted to obtain optimal sampling results for each stream. Sampling started downstream, and depending on stream width two to five people processed slowly on the same level upstream while dip-netting preferably all tadpoles and invertebrates in all microhabitats. We kept tadpoles alive and carried them in water containers in the laboratory. They were euthanized by immersion in chlorobutanol solution, and immediately sorted into series based on their morphology. From each series, we identified one specimen by DNA barcoding based on a fragment of the mitochondrial *16S* rRNA gene (Vences et al., 2005; Vences et al., 2008). DNA sequences of all 1472 identified tadpole series (corresponding to 7020 individuals of 36 species, 2-18 species per stream) are deposited in Genbank (accession numbers FJ217329-FJ217345, GQ904717-GQ904746, GU808474-GU808492, GU974370-GU975745).

For all species present in the streams, we constructed a trait matrix based on morphological features that are known to be of ecological relevance (Table 1). By influencing basal resources and primary producers mainly due to foraging, tadpoles affect primary production and eventually stream ecosystem structure and function (Ranvestel et al., 2004; Connelly et al., 2008). We therefore focused on ecological traits related to where and how tadpoles forage in the stream, and

as a proxy for these we selected adequate morphological traits for analysis. We included features of oral disc shape, the shape of jaw sheaths, and presence of keratodonts as these traits are related to tadpole feeding (Altig & Johnston, 1989; Harris, 1999). We also used values for papillae and measurements of body shape as they are related with tadpole microhabitat (Altig & Johnston, 1989; Alford, 1999; Hoff et al., 1999).

## Statistical analyses

*Ordination of environmental variables* – We applied Principal Component Analysis (PCA) to reduce the dimensions of explanatory variables to a smaller set of orthogonal synthetic variables. We performed PCA on all 14 original habitat variables (see above) and for the 29 streams, on the correlation matrix in order to standardise for the influence of unequal variance. To evaluate data outliers and linear interdependence of variables, we used box-plots and pair-plots, respectively (Zuur et al., 2007) (see additional file 2: data evaluation). As outliers can affect the outcome of the PCA, we reduced their influence by applying box-cox-power-transformations (Box & Cox, 1964) on habitat variables containing outliers. An assumption of PCA is linearity and evaluating pair-plots, we found no obvious non-linear relation in the habitat variables. We assessed the significance of the PC loadings based on the bootstrapped-eigenvector method as suggested by Peres-Neto et al. (2003). We estimated the number of meaningful PCs by a scree plot (Zuur et al., 2007). We conducted multiple linear regressions with the first three PCs as independent variables and species richness as response variable (without interaction). Residuals of this and all other regression analyses were checked for patterns e.g. of heteroscedasticity, normality or highly influential data points using diagnostic plots (see additional file 3: diagnostic plots).

*Species diversity* – We assessed species richness (SR) in stream sections based on molecular identification of tadpoles sampled. We calculated functional diversity (FD) following the methodology of Petchey & Gaston (2002b, 2006). This is a three-step dendrogram based classification function, in which a species trait matrix is used to calculate a pair-wise species distance matrix, which is used to construct dendrograms of specific species assemblages.

**Table 1** Ecological traits and the representing morphological traits of tadpole species used for calculating functional diversity.

| Ecological trait | Morphological trait | Type of data |
|---|---|---|
| feeding and ability of habitat use by shape of oral disc | mouth opened | binary |
| | umbelliform | binary |
| | suctorial | binary |
| | generalised or small but with keratodonts | binary |
| | reduced | binary |
| | generalised | binary |
| feeding type (e.g. filterer, grazer, carnivore) represented by jaw sheaths shape | generalised | binary |
| | keratinised, vertical bars | binary |
| | poorly keratinised | binary |
| | transformed in a three sporn-shaped papillae | binary |
| | transformed in bow-net structure | binary |
| | absent | binary |
| feeding type | number of keratodonts rows | continuous |
| habitat use (adaptations to water current) | number of papillae | continuous |
| | relative oral disc width | continuous |
| | relative tail muscle height | continuous |
| | relative tail length | continuous |
| habitat use (use of the water column) | eye position | binary |

The total branch length needed to connect all species in the assemblage represents the respective FD. There is a variety of distance measures and cluster methods available, however, there is no general rule of which methods perform best (Mouchet et al., 2008). As our trait matrix, consisting of morphological traits of tadpoles (Table 1), contained both categorical and continuous variables, we used Gower's distance. We identified unweighted pair group method using arithmetic averages (UPGMA) as the best cluster method for our dataset, using an automated selection procedure implemented in the "GFD" script of Mouchet et al. (2008). GFD selects the combination of distance and clustering algorithms that best fits the species distribution in the functional trait space by minimizing the dissimilarity between the distance matrix and the

ultrametric matrix of the functional tree. GFD calculates all the possible consensuses and simple dendrograms and selects the best by confronting them to the initial distance matrix. We applied polynomial regression of observed FD values as response and SR as independent variable to test for coherency and patterns of species redundancy (non linearity). For polynomial regression, higher powers of the explanatory variable are fitted to a linear model, and the significance of the new explanatory term is assessed by multiple regressions. Significant results show non-linearity in the data. To judge the level of FD of tadpole communities, we calculated a predicted value of FD for each observed community according to its SR level and compared these with the observed FD along a SR gradient. Each predicted FD value is the calculated mean of the FD of 500 randomly assembled communities. These were random assemblies chosen from all 36 species sampled in the study area, controlled for number of species. Due to non-normal distribution and violation of independence of residuals in the linear model for the predicted FD of the random communities, we used non-linear least-squares estimates of parameters of non-linear regression models describing an ascending asymptotic hyperbola (Michaelis-Menten kinetics). Such an asymptotic increase of FD can be expected by increasing SR in communities (Fonseca & Ganade, 2001; Petchey & Gaston, 2002a, b; Halpern & Floeter, 2008) and describes a FD-SR relationship with functional redundancy. Similar to an ANCOVA for linear relations, we used FD as the response variable, SR as the predictor and a binomial predicted-observed-variable as covariate (factor), and performed a t-test on the coefficients. We compared curve progression of observed and predicted FD data to access environmental impacts on species similarity within communities.

We used morphological traits, especially characters of oral disk and body shape (Alford, 1999) as proxies for resource use, including food and habitat choice of the tadpoles (Table 1) because no direct information on their diet and behaviour exists. Respective morphological data were sourced from publications (Raharivololoniaina et al., 2006; Glos et al., 2007; Randrianiaina et al., 2009; Schmidt et al., 2008; Schmidt et al., 2009; Grosjean et al., accepted). If lacking a published description, they were assessed from the sampled specimens using a Zeiss StereoDiscovery microscope with Zeiss AxioVision software.

We performed all analyses in R 2.9.0 (R Development Core Team, 2009). The code for bootstrapped-eigenvector method is courtesy of J. Oksanen. The Xtree function and further codes required for calculations of FD are courtesy of O. Petchey. The GFD code to identify the best distance measure and cluster method for FD calculation as well as their application following Mouchet et al. (2008) was provided by the authors. In addition, the following packages were used during the analyses: car (Fox, 2008), clue (Hornik, 2009), cluster (Maechler et al., 2005), gtools (Warnes, 2009), lattice (Sarkar, 2008), and nlme (Pinheiro et al., 2008).

# Results

### Habitat ordination

We could summarise the 14 original habitat variables to three PC factors (according to the scree plot) with PC1 representing 49.9 %, PC2 22.8 %, and PC3 13.0 % of the original variation. Bootstrapping-eigenvector method highlighted these habitat variables as significantly contributing to PC1: stream *slope* (–), stream *canopy cover* and forest *CANOPY COVER* (–), *SHRUBS* (–), and the stream microhabitats *sand* (–) and *leaves* (–) as well as *rock* (+) and *gravel* (+), stream *width* (+), *mayfly larvae* (+) and *dragonfly larvae* (+) (Figure 1). For PC2 this were stream *width* (–), stream microhabitat *sand* (–), and *dragonfly larvae* (–) as well as stream *slope* (+), and the stream microhabitats *rock* and *gravel* (+) (Figure 1). The strongest contributions to the PC3 come from forest *LEAF LITTER* (–), forest *CANOPY COVER* (–), and forest *TREES* (+), however, the results were not significant.

PC1 therefore represents a gradient from smaller streams with a generally dense canopy cover and a high proportion of microhabitats consisting of leaf and sand substrate towards larger streams with a higher proportion of gravel and rock substrate and higher invertebrate larvae abundances. This gradient is highly significant and positively correlated with SR (multiple linear regression, $F_{2,26} = 50.75$; $R^2 = 0.80$, $p_{model} < 0.001$; $p_{PC1} < 0.001$). PC2 represents a gradient from larger, slow-moving and sandy streams with high abundance of dragonfly larvae towards small and rocky streams with steep slopes. This gradient is highly significant and negatively correlated with SR ($p_{PC2} < 0.001$). As the third PC was not correlated to SR, it was removed from the model in order to find the minimal adequate model.

We overlaid a PCA biplot with SR (Figure 1), which illustrates a gradient of increasing SR from the top left corner to the bottom right corner (for alternative graphical illustration see additional file 1: regressions of PCs vs SR). Accordingly, SR increases mainly with stream *width* and *dragonfly larvae*, and decreases with stream *slope*, stream *canopy cover* and forest *CANOPY COVER*. The proportion of specific stream microhabitats (i.e. stream substrates) did not have a major impact on SR.

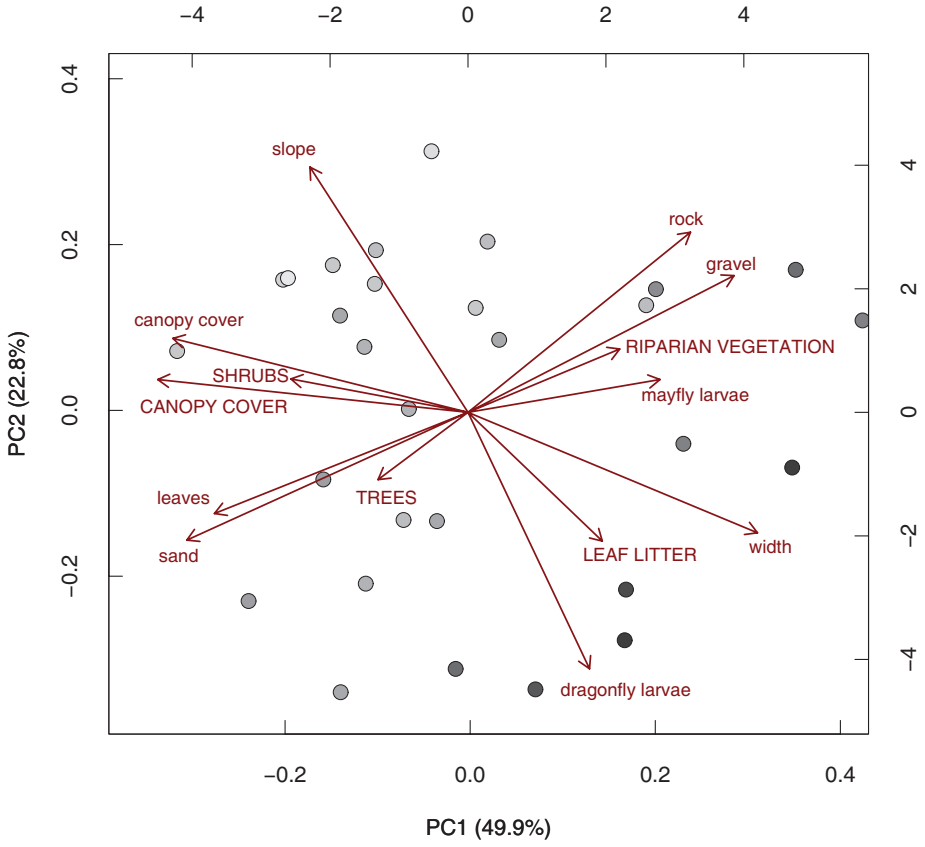


**Figure 1** Principal component biplot showing PC1 and PC2. Vectors show the environmental variables, tadpole habitat characteristics are in lower case, adult frog habitat parameters are in capital letters. Filled circles represent study sites (streams) that are plotted according to their scores (pay attention to scales). Symbols are coded by continuous grey shading showing low SR (light grey) to high SR (dark grey).

## Functional diversity (FD)

Applying a polynomial regression model, we found a highly significant positive correlation between SR and FD ($F_{1,27} = 209$, $R^2 = 0.89$, $p_{model} < 0.001$, $p_{SR} < 0.001$). Although the increase of $R^2$ (0.89 vs. 0.91) was low, the included quadratic term still significantly contributed to the model ($F_{2,26} = 124.3$, $R^2 = 0.91$, $p_{model} < 0.001$, $p_{SR} < 0.001$, $p_{SR^2} = 0.028$, Figure 2). This correlation is therefore not linear but shows a decreasing slope with higher SR. This pattern expresses an increase in functional redundancy of tadpole species with increasing SR of the stream community.

The predicted FD of random communities showed a similar pattern (Figure 2). Due to violation of independence of the residuals we could not fit a linear model for predicted FD and therefore applied Michaelis-Menten with parameter estimates for maximum FD and the SR of communities with mean FD to compare curve progression of both predicted and observed data. This non-linear regression model and t-tests applied on the parameter estimates show that the maximum FD for the observed communities (FD = 1.11±0.07) was significantly lower than the maximum predicted FD for the random communities (FD = 1.21±0.08; t-test, $t = -9.501$, $df = 54$, $p < 0.001$). There was no difference in SR values at a mean FD between observed (S = 11.12±1.32) and predicted communities (S = 12.06±1.40; t-test, $t = 6.275$, $df = 54$, $p = 1$).

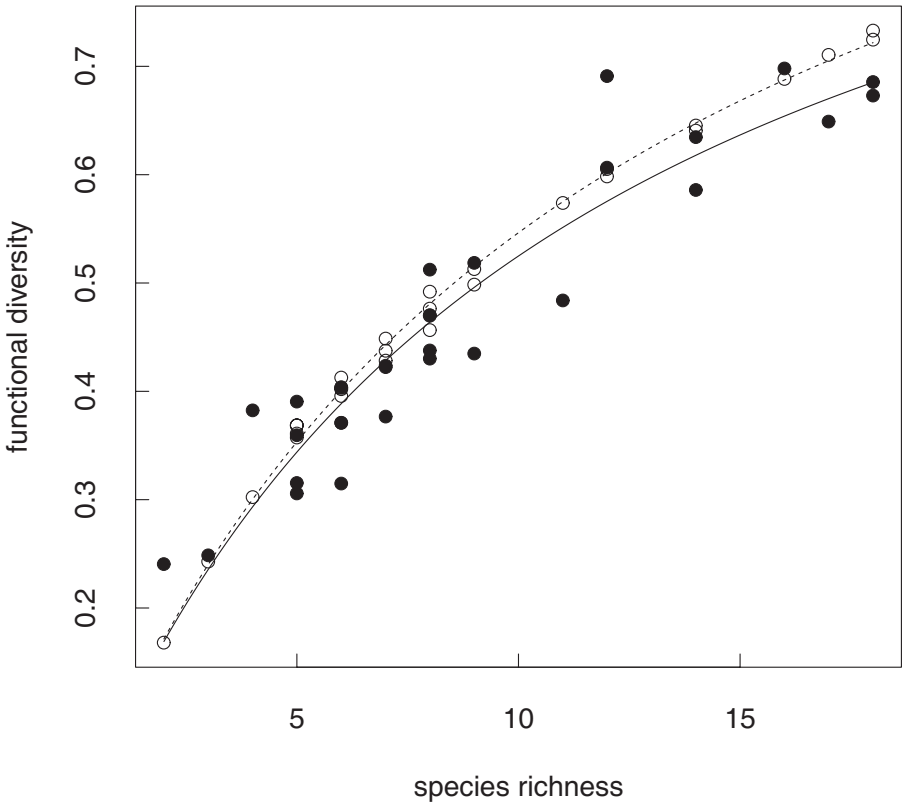


**Figure 2** Comparison of predicted (black circles, dashed line) and observed functional diversity (FD, filled dots, continuous line) along species richness. Predicted FD calculated from simulated random assemblages. Lines show the fitted non-linear regression.

These tests and the graphical evaluation (Figure 2) describe a pattern of low functional diversity but only in species-rich communities.

# Discussion

### Madagascan streams as tadpole hotspots

Madagascan rainforest streams harbour the world's most species-rich tadpole communities. In 30 m sections of RNP mid-elevational rainforest streams in the current study, species richness (SR) of tadpole assemblages varied from two to 18 species, with an average of nine species and a total number of 36 species. At another site in Madagascar, An'Ala rainforest in central eastern Madagascar, an even higher number of species was reported with a maximum of 28 species in a 50 m stream section (Vences et al., 2008). Distinctly lower numbers of species were reported from tropical streams in Brazilian forests (1-8 species, (Hero et al., 2001); 1-9 species, (Afonso & Eterovick, 2007); 2-10 species, (Eterovick, 2003)). Equally remarkable is that the Malagasy stream tadpole communities can be impressively rich in specimens. We detected up to 1,100 tadpole individuals per 30 m of stream which emphasises their high importance for the Malagasy stream ecosystems and claims for explanations beyond a simple correlation with frog species richness. In fact, the number of frogs in both RNP and the Mantadia-Analamazaotra area (including An'Ala

forest) is around 100 species which is very high but not markedly different from other tropical amphibian hotspots (Vieites et al., 2009). However, Madagascan rainforests show a higher proportion of stream-breeding frog species than other tropical amphibian communities which often contain many pond breeders. In general, Madagascan rainforests along the geographically steep eastern escarpment do not offer many pond breeding habitats which explains the low number of pond breeding species. There is little information available on species breeding in phytotelmata, tree holes or foam nests on the forest floor but we assume their relative frequency is low.

We also consider the virtual absence of fish possibly a main reason for the exceptional tadpole diversity and abundance in Madagascan rainforest streams. Both RNP and An'Ala, and Madagascan rainforest streams in general, are exceptional among tropical rainforest streams in their remarkably low density and diversity of fish. In most RNP streams, only the eel (*Anguilla* sp.) occurs in detectable although very low numbers.

### Tadpole diversity is dependent on stream size and velocity

Tadpole diversity is not explained by those habitat variables that are important for adult frogs. Neither the forest structure around a stream nor its streamside vegetation structure correlated significantly with tadpole SR. This shows that tadpole diversity is not limited by environmental filters that affect adults and that might cause streams not being used for breeding although they might represent suitable habitat for tadpoles.

In contrast, those habitat variables that directly act on tadpoles explain tadpole diversity very well. Based on the results of the PC and regression analyses, diversity concerning both, SR and FD, increases along a stream size-velocity gradient, i.e. it was highest in slow moving (low *slope*), large streams, with open canopy cover, and a high abundance of dragonfly larvae. The proportion of specific ground substrates within the streams was not important.

The observed stream size – SR dependency follows a general ecological pattern, i.e. the species-area relationship that is found very commonly for a wide variety of taxa and types of ecosystems, and only few exceptions exist (e.g. Dunn & Loehle, 1988). In fact, the species-area relationship is often referred to as the closest thing to a rule in ecology (Lomolino, 2000). It states that along a gradient of ecosystems of increasing size, the numbers of species inhabiting those ecosystems increase, in general rapidly at first, and then more slowly for the larger ecosystems. However, many tadpole communities and their ecosystems, e.g. streams and ponds, are among the exceptions. For stream habitats studies on the dependencies of stream size and tadpole diversity are inconclusive. Both positive and negative continuous relationships are found, i.e. the most

diverse communities are in the largest (Parris & McCarthy, 1999) or in the smallest streams (Afonso & Eterovick, 2007; Eterovick, 2003). For tadpole communities of tropical ponds, as a general pattern, tadpole SR increases with increasing pond size, but beyond a certain size, ponds are permanent (vs. temporary), and an increasing number of fish eliminate tadpoles. This results in medium-sized water bodies harbouring the highest number of tadpole species (Heyer et al., 1975). Our rainforest stream data are generally consistent with the predictions derived from these studies on ponds, although there is no peak in SR at an intermediate stream size. All the streams in the current study are permanent, and as a peculiarity, fish are not an important factor for tadpole survivorship. Therefore, factors that limit SR beyond a certain water body size may thus not be effective in RNP tadpole communities.

The increase of SR along the stream size-velocity gradient cannot be attributed unambiguously to a higher number of different microhabitats in larger habitats. All microhabitats, i.e. ground substrates, were present in all streams, and their respective proportions were not significantly correlated to SR. High stream velocity, in contrast, might be a factor limiting SR. Of the species occurring in the RNP region, only a few have morphological adaptations to strong currents (Glos et al., 2007; Randrianiaina et al., 2009) and high currents might prevent some species from colonising streams. In general, selective pressures caused by stream current can be hypothesised to be stronger in fast-running portions of the streams, where tadpoles not adapted to such conditions will be washed away during high flow levels after heavy rain. In contrast, in slow-moving stretches, tadpoles adapted to stronger currents will be able to survive, even if they may suffer from increased competition with other larvae better adapted to these conditions.

### FD and functional redundancy are dependent on species richness

We found both functional redundancy and low FD in tadpole communities of Madagascan rainforest streams. The presence of functional redundancy indicates an overlap in the traits of species within a community. While this can be interpreted as dispensability of some species, it is also a buffer to ensure community resilience (Walker, 1995; Rosenfeld, 2002). Patterns of redundancy have been reported when using functional groups e.g. for bat (Stevens et al., 2003), plant (Fonseca & Ganade, 2001; Mayfield et al., 2005; Halpern & Floeter, 2008), bacterial soil communities (Yin et al., 2000), and coastal marine assemblages (Micheli & Halpern, 2005). However, the functional group approach highlights only some functions of species and disregards a possible wide range of others. As focusing on few traits likely leads to findings of patterns of functional redundancy (Fonseca & Ganade, 2001; Petchey & Gaston, 2002b), we used a continuous measure using 18 morphological traits relating differently to habitat use and feeding

ecology (Table 1) to include a wide range of species functions that can influence stream ecosystem structure and function.

Previous identification of functional redundancy quantified by continuous FD were generally attributed to agricultural landscapes or anthropogenic disturbed sites (Flynn et al., 2009; Ernst et al., 2006). We here show, however, that functional redundancy is also an attribute of communities in primary freshwater stream habitats. Whereas a linear but only slightly increasing relationship between SR and FD shows a continuous pattern of redundancy, the curvilinear shape observed for tadpole communities shows that functional redundancy depends on the level of SR, with the highest functional redundancy assigned to species-rich communities in large streams. We here face the world's most species-rich communities, however, compared to many other ecological systems, the absolute number of species is relatively low. For example, functional diversity studies on plant communities may include 11 to 75 species per community (Mayfield et al., 2005), a study on deep sea nematode assemblage up to 80 species per site (Danovaro et al., 2008) and up to almost 480 species per site in a reef fish study (Halpern & Floeter, 2008). Identification of potential SR-FD relationships may be difficult using only a low SR or low range of SR (Petchey et al., 2007; Halpern & Floeter, 2008). The range of SR of tadpole communities is obviously sufficient to detect patterns, as indicated both in the curvilinear FD curve and the species richness dependent functional redundancy (discussed below). The fact that functional redundancy and low FD of tadpole communities are not very pronounced compared to other studies (e.g. Halpern & Floeter, 2008) still supports the need of a sufficient range of SR for studies on FD (Halpern & Floeter, 2008). Facing adult frog plus tadpole traits and using about twice the number of species as in the present study (up to 39 per site and 55 in total) showed quite clear patterns of redundancy in West Africa (Ernst et al., 2006). However, studying a large number of species often implies a large geographical study area (e.g. Stevens et al., 2003; Halpern & Floeter, 2008). Consequently, using all ecological species traits available in the whole geographical range for random FD calculations and thereon depending comparisons with observed data may lead to patterns of e.g. low FD that are difficult to assign to either ecological or geographical filters, or both.

We could show that with increasing SR, the FD of tadpole communities was increasingly lower than the FD of randomly assembled communities of similar SR levels. This difference between observed and predicted FD values shows low FD and indicates that members of species-rich communities were more similar to each other than expected by random assembling. Low FD was observed in bird (Petchey et al., 2007), plant (Mayfield et al., 2005) and reef fish communities (Halpern & Floeter, 2008), however, only the latter showed a similar SR-dependent pattern. This is an indication of SR dependent environmental filtering (Petchey et al., 2007) and whereas up to

a certain level of SR the assemblage of different traits of tadpoles is random, in richer communities stream-specific traits accumulate. As discussed above, low FD in tadpole communities is statistically significant but still not as pronounced as e.g. in reef fish communities (Halpern & Floeter, 2008). However, differences in the geographical ranges in the studies and the resulting difficulties of interpretation complicate the comparison of studies. If competition is a shaping force, species characterised by dissimilar traits would form a community, resulting in high values for FD (Petchey et al., 2007). This was not the case for any level of SR. As we used traits for calculation of FD related to habitat use and foraging of tadpoles, we conclude that interspecific competition for space and food does not influence the composition of tadpole communities in Madagascan rainforest streams. It is habitat characteristics of the stream and/or the (non-)availability of food that filters specific traits and therefore specific species from communities, at least in species-rich large streams.

## Conclusions

In summary, (1) SR of Madagascan stream tadpole communities generally follows a species-area relationship leading to the worlds highest number of tadpole species, (2) evidence from these communities shows occurrence of functional redundancy in primary freshwater habitats, and (3) environmental filtering but not interspecific competition may be a major factor influencing assembly of tadpole communities. We could prove both findings of functional redundancy and low FD associated with high SR for reproducibility by repeated sampling of streams in RNP in 2008 (own unpublished data). These results highlight the potential of FD to provide insights into the under-investigated communities of larval stages of anurans. We see particular promise in future studies that integrate these findings with further community characteristics such as food web structures, and we predict these will help elucidating the fundamental processes that structure amphibian communities.

## Authors' contributions

AS participated in the design of the field study, conducted field work, designed and conducted statistical analyses, evaluated DNA barcoding results, and drafted the manuscript. ER conducted fieldwork and morphological analyses and contributed in discussions on the manuscript. RDR conducted fieldwork and conducted most of morphological measurements. MV designed the morphological and the DNA barcoding part and significantly developed the draft. JG designed the field study, conducted fieldwork, was substantially involved in the design of the statistical analyses and in the discussion of the results, and significantly developed the draft. All authors read and approved the final manuscript.

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# Additional files

Additional files are available for this chapter. Due to their size, they were not included in the printed version of this work. Below is a description of the files, and we provide links to the freely accessible files.

**additional file 1**
title: regressions of PCs vs SR
[http://www.biomedcentral.com/content/supplementary/1472-6785-10-12-s1.pdf]
description: Plots for visual evaluation of the multiple regressions of Principal Components and species richness (SR). (A) to (C) display the regressions of SR depending on PC1 to PC3, respectively. PC3 was removed from the model and PC1 and PC2 remained. A summary of the correlation of SR and PC1 and PC2 is given in Figure 1 by a grey shading of the symbols.

**additional file 2**
title: data evaluation
[http://www.biomedcentral.com/content/supplementary/1472-6785-10-12-s2.pdf]
description: Data evaluation of habitat variables used for Principal Component Analysis. Tadpole habitat characteristics are in lower case, adult frog habitat parameters are in capital letters. (A) Box-plots of the original and the transformed (with the extension "box-cox") habitat variables. We used these plots to evaluate data regarding outliers and extreme values that might influence the results of the PCA. We tried to minimise the influence of outliers on PCA by applying box-cox transformations on the original variables. Box-plots of transformed habitat variables are displayed next to the respective original habitat variable.
(B) Pair plots of the habitat variables. We used these pair plots to evaluate data regarding strong non-linear relations between the habitat variables and extreme values in the multivariable space after data transformation.

**additional file 3**
title: diagnostic plots
[http://www.biomedcentral.com/content/supplementary/1472-6785-10-12-s3.pdf]
description: Diagnostic plots used for model evaluation. Generally, panels 1 and 3 show residuals versus fitted values, panels 2 QQ-plots for normality, and panels 4 show standardised residuals vs. leverage and Cook statistics. (A) and (B) show diagnostic plots for the regression of observed functional diversity (FD) and species richness (SR) for the simple linear model (panels A1–4) and the quadratic model (panels B1–4). There were weak patterns in panels A1 and A2 which are reduced in panels B1 and B2. (C) and (D) show diagnostic plots for the regression of predicted FD of random communities and SR for the simple linear model (panels C1–4) and the quadratic model (panels D1–4). Note the very strong patterns in all C panels. Also in the quadratic model (D panels), strong patterns remain: D2 still shows non-normality in the residuals. Whereas D1 and D3 seem to show homogeneity in the data, they still show a violation of independence and D4 identifies highly influential points. We therefore desisted from applying a linear model on these data. (G) shows the residual plot to evaluate the non-linear regression of FD and SR. There is no obvious violation of homogeneity or independence.

# Seasonal changes act differently on functional and phylogenetic diversity of Madagascan tadpole communities

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## Abstract

Communities that are exposed to recurring environmental changes show changes in their properties. These can be expressed by differences in diversity and community assembly rules. Both can be "identified" using two useful measures of diversity: functional (FD) and phylogenetic diversity (PD). We utilised tadpole communities from Madagascan rainforest streams to identify such effects of seasonal changes. From the wet to the dry season, species richness (SR) of tadpole communities decreased. Also FD and PD decreased, but FD less and PD more than expected. During the dry season, tadpole communities were characterised by functional redundancy, high functional diversity, and phylogenetic clustering. As a main result, communities are driven by competition but only in the dry, not in the wet season.
The supposed discrepancy of species being less similar but closer related than expected may be due to physiological or behavioural traits that were not considered for FD.

Keywords: tadpoles, amphibian, species richness, functional diversity, phylogenetic diversity, relatedness, extrinsic redundancy, phylogenetic clustering, phylogenetic overdispersion, seasonality, tropics, Madagascar

## Background

The properties of species communities vary in time. On an ecological time scale, these variations might be anthropogenic, caused by drastic single events (e.g. fire), or recurring due to annual climatic changes (Rosenzweig, 1995; Huston, 1995; Moretti et al., 2009; Dinnage, 2009). Most obviously, changes in species communities are reflected by changes in species richness (SR). However, SR as measure of diversity is likely to miss relevant information on diversity because the species that make up a community are connected to each other regarding their ecological traits and regarding their phylogenetic relatedness. Also these two variables are not necessarily congruent (Prinzing et al., 2008; Cadotte et al., 2009). Ecological traits of species (and therefore the functional diversity of communities, FD) can determine their habitat depletion, coexistence and may reflect ecological impact of communities, e.g. biomass production (Joshi et al., 2000; Scherer-Lorenzen, 2008; Hoehn et al., 2008). The degree of relatedness (summarised as the phylogenetic diversity of a community, PD), is an alternative measure of community structure and ecosystem process (Cavender-Bares et al., 2009). Being independent on previously chosen

ecological traits, it can (Cadotte et al., 2009) but not necessarily does (Cadotte et al., 2008) even outperform functional diversity as determinant.

Non-congruency between FD and PD can be caused by different factors. It is often assumed that closely related species show a high degree of morphological and ecological similarity (Harvey & Pagel, 1991). There can indeed be a strong similarity between sister species (Grosjean et al., in press), but closely related species can also be morphological and ecological divers. On the contrary, there can also be a high degree of homoplasy (Wake, 2009).

A focus on FD rather than SR allows measuring the overlap in ecological traits between species and therefore identifying intrinsic functional redundancy of communities (Walker, 1992, 1995; Petchey et al., 2007) whereas PD identifies intrinsic phylogenetic redundancy. If the environmental conditions of communities change, compositional changes may affect FD and PD in a different way than it would affect SR. Given intrinsic functional redundancy (sensu Petchey et al., 2007), a random gain or loss of species will have lower effect on FD than on SR (Petchey et al., 2007), and PD will be less affected if intrinsic phylogenetic redundancy exists. Intrinsic redundancy is present regarding species function in a range of disturbed (Flynn et al., 2009; but see Micheli & Halpern, 2005; Petchey et al., 2007) and undisturbed (Strauß et al., 2010) ecosystems across several taxa and regarding relatedness in urban plant communities (Knapp et al., 2008).

Another kind of redundancy can be observed if the changes in SR are non-random with respect to species traits and/or relatedness. This so called extrinsic redundancy (Petchey et al., 2007) can occur if certain species traits are positively or negatively selected under certain conditions. Species may appear or disappear from a given community that are more functionally similar or different to each other than expected given a certain species pool available and a random change in species composition. This can be caused by environmental filters or competition and results in high or low FD regarding functional traits (Petchey et al., 2007) and phylogenetic overdispersion or clustering regarding relatedness (Horner-Devine & Bohannan, 2006; Emerson & Gillespie, 2008). Examples for extrinsic redundancy are observed in directly human influenced systems across several animal and plant taxa (Flynn et al., 2009; Ernst et al., 2006; Sasaki et al., 2009).

Beside single disturbance events, such as fires and logging, environmental conditions can also vary by annual climatic changes. Their recurring influence should have established adapted processes of changes in community composition. The existence and strength of seasons are of importance for community assembly (Inger et al., 1986). Whereas seasonal changes can be very pronounced, they can also be restricted to a certain limit, especially in tropical regions. This enables the existence of comparable species community structures throughout the year (Crump, 1974).

Patterns of seasonal differences in SR in the tropics are known for numerous (DeVries & Walla, 2001; Nicolas & Colyn, 2003; Andreone, 1996; Kopp & Eterovick, 2006; Pereira et al., 2009) but not all groups of small animals (Grimbacher & Stork, 2009). It is poorly explored how this recurring environmental disturbances act on species traits or relatedness of communities, although species show specific reactions on seasonality depending on some ecological characters (Gottsberger & Gruber, 2004; Grimbacher & Stork, 2009). It may therefore be important for understanding processes shaping species assemblages, e.g. competition or environmental filters, to turn attention not only on the season that is expected to be best for the taxon.

Tropical anuran communities represent an appropriate model to study seasonal changes and their impact on different measures of diversity as they are known to be remarkably rich but still can be completely assessed and taxonomically handled (Vieites et al., 2009). Seasonal changes in SR have been observed for adult amphibian (Andreone, 1996; Kopp & Eterovick, 2006), and to some extend for amphibian larvae communities (Both et al., 2009; but see Afonso & Eterovick, 2007).

Another important point is that also for amphibian larvae the general rule applies that morphological features reflect phylogenetic history (Haas, 2003). Beside this generality, homoplasy can be observed (e.g., umbelliform oral discs in *Chonomantis* and Megophryinae (Grosjean et al., in press), and reductions of oral disc in some *Boophis* and *Ochthomantis* (Randrianiaina et al., submitted)). And whereas some phylogenetic groups show strong morphological and ecological similarity (Grosjean et al., in press), other groups have evolved a high diversity (e.g. in the mantellid *Boophis majori* group). However, these exceptions from the rule are randomly distributed and differences between FD and PD are possible but not enforced.

That FD is a valuable measure of diversity of tadpole communities providing additional information to SR has been shown before (Strauß et al., 2010). It is, however, so far not known how annual changes act on FD. Furthermore, whether PD provides similar information as FD or not has neither been investigated for tadpoles or other animals with a biphasic life cycle nor with a focus on seasonal changes.

We utilised the world's most species rich stream tadpole communities (Strauß et al., 2010) to evaluate patterns of SR, FD and PD during two seasons in mid-elevational rainforest of Madagascar. We expected species richness to be lower in the dry season than in the wet season, following the pattern observed for adults (Andreone, 1996). We assumed four scenarios of changes in FD and PD as possible: (1) FD and PD change congruent to SR. There is no or only weak indication of extrinsic or intrinsic redundancy or a lack thereof. (2) Tadpole communities are characterised by intrinsic redundancy in the wet season (Strauß et al., 2010). The loss of species due to less suitable climatic conditions towards the dry season occurs randomly and FD

and PD change therefore less than expected. (3) The loss of species occurs non-random with respect to species traits and relatedness. Given a strong phylogenetic signal in the traits, both FD and PD may change or not, but different to SR. For example, at first species disappear that share common traits of the community. This can be due to increasing competition caused by reduced resource availability; consequently, FD and PD change less that SR. This can also be due to environmental filters, and only species sharing specific trait combinations remain throughout the year. This extrinsic sensitivity causes changes in FD and PD being more pronounced than changes in SR. (4) The loss of species occurs non-random with respect to species traits and relatedness but FD and PD change in different ways. This may happen if PD covers more or different tadpole traits than included in FD, or PD represents traits of adults rather than of tadpoles.

# Methods

### Study sites

We conducted two sessions of fieldwork, in the wet season (January and February) and in the dry season (July) of 2008. Study sites were located in one of the centres of amphibian species richness in Madagascar, Ranomafana National Park (RNP; 21°16'S; 47°25'E; 500 – 1500 m a.s.l.). RNP covers over 40,000 ha of rain forest from ca. 500 m up to ca. 1.500 m a.s.l. and harbours over 100 frog species (Vieites et al., 2009). Seasonality in this area is only of certain extent with differences in precipitation and strong differences in temperature, having consequences on species richness in adult frogs (Andreone, 1996).

### Species sampling

We sampled tadpole communities of 30 m sections of 12 streams (in a mid-elevational area ranging from 910 m to 1.130 m a.s.l.) using dip nets of different size and materials, adjusted to obtain optimal sampling results for each stream. Sampling started downstream, and depending on stream width two to five people processed slowly on the same level upstream while dip-netting. We kept tadpoles alive and carried them in water containers in the laboratory. They were euthanized by immersion in chlorobutanol solution, and immediately sorted into series based on their morphology. From each series, we identified one specimen by DNA barcoding based on a fragment of the mitochondrial *16S* rRNA gene (Vences et al., 2005; Vences et al., 2008). DNA sequences are deposited in Genbank [sequences are in the process of preparation for submission

to Genbank]. This process was done once in the wet and once in the dry season, applying the same sampling methods to the same stream sections. All comparisons are based exclusively on tadpole data which are a reliable representation of the frog species actually breeding in a single stream; sightings of adults were not considered.

We tracked changes of water temperature during the seasons by placing temperature loggers (Thermochron® iButton, Dallas Semiconductor) in the streams one year before this study. They were set to conduct measurements every 255 min covering about one year (early 2007 to early 2008). Data on aerial temperature and rainfall were provided ValBio research station, Ranomafana (J. C. Razafimahaimodison).

### Statistical analyses

We assessed species richness (SR) of tadpole communities in dry and wet season based on molecular identification of tadpoles sampled. We first confirmed the expectation that species richness (SR) of tadpole communities differs between wet and dry season by paired t-test. Before testing whether changes in FD or PD are similar to changes in SR or whether species loss and turnover depend on the ecological function of species, we developed a null model. For this null model, we remodelled random communities of wet and dry season, based on observed SR, observed changes in SR, observed species turnover, and the observed species pool available for each stream. In detail, for each stream we pooled all species found in wet and/or dry season in this stream and reordered them randomly 1000 times. Out of these 1000 pools, we each picked the first x species (with x being the number of species observed for this stream in the wet season) and thus achieved random communities for the wet season. To achieve random communities for the dry season, we first each picked the remaining y species that were not already included in wet season communities (with y being the number of species that were found in the dry but not in the wet season in this stream) and then restocked by randomly chosen species from the respective random wet season community to reach the final number of species for the random dry season community as observed. This was repeatedly done for each stream based on the species that we observed in the stream. For each stream and season we first calculated predicted FD of the communities in the seasons and then the predicted change in FD from the wet to the dry season.

FD was calculated following Petchey & Gaston (2002, 2006). This is a three-step dendrogram based classification function, in which a species trait matrix is used to calculate a pair-wise species distance matrix, which is used to construct dendrograms of specific species assemblages. The total branch length needed to connect all species in the assemblage represents the respective FD. Best distance measure (Gower's distance) and cluster method (UPGMA) have been

identified following Mouchet et al. (2008). Our trait matrix consisted of categorical and continuous morphological trait variables (oral disc, body shape) of ecological relevance (i.e. feeding, microhabitat choice) (Alford, 1999) for all species (for a list of traits used, see Strauß et al., 2010).

To find a function representing the null model for changes in FD depending on changes in SR, we conducted polynomial regression with predicted FD as dependent and SR and its polynoms as independent variable to prove whether these variables are correlated, whether a correlation is linear and whether a predicted correlation differs from a simple predicted 1:1 relation (Micheli & Halpern, 2005; Petchey et al., 2007). Based on these results we used models based on our predicted FD values as null models for further analyses.

We calculated FD and the changes in FD for the observed communities. As for predicted FD values, we conducted polynomial regression with changes in SR and its polynoms as independent variables. We did this primarily to assess the shape of the change, i.e. whether there is non-linearity. To test whether the results (observed change of FD) differs from the null model, for each community we calculated the deviation of observed and predicted changes in FD and performed a one-sample t-test. Significant results show that seasonal changes in FD are not random.

Non randomness must be due to changes in patterns in redundancy between the seasons or due to high or low FD in one or both seasons (Petchey et al., 2007). We therefore analysed data of the wet and the dry season separately. We again proofed that predicted FD provides a better null model than a simple 1:1 model for a SR – FD relation, as we did for the changes in SR and predicted FD. Polynomial regression with observed FD as dependent and SR as independent variable allows conclusions on possible patterns of functional redundancy in the single seasons (if non linearity is found).

We again calculated the deviation of the observed FD data from the null model and performed one-sample t-test, once for each season. This allowed identifying possible patterns of low or high FD in the tadpole communities, if results were significant.

Anurans show a biphasic life cycle and both stages may be of importance to understand FD – PD – SR relations of tadpole communities. Therefore, we also created a matrix of adult traits and performed FD analysis as stated above. The adult traits included are given in Table 1.

We conducted the same procedure to analyse patterns of phylogenetic diversity (PD), respectively their changes from wet to dry season. As basis for predicted PD, the same random communities were used as for the calculations of FD. Our analyses are based on a time-calibrated phylogeny of mantellid species (K. Wollenberg, unpublished manuscript), as all tadpoles sampled in the streams belonged to this family (Strauß et al., submitted). Out of this

tree, we extracted a subtree including all species relevant for this seasonal comparison of PD using TreeEdit version v1.0a10. This reduced the number of species by retaining branch length. As for a few so far undescribed species genetic data were insufficient to include them in the tree, other species that are known to be in the same clade (according to molecular data of Vieites et al., 2009) were used as replacement for the purpose of PD calculation. Similar to FD calculations (Petchey & Gaston, 2002, 2006; Podani & Schmera, 2006), we extracted branch length from the tree for the communities by using the function treedive included in the R package vegan, version 1.15-4 (Oksanen et al., 2009). The branch length needed to connect all species of a community represents the community's PD.

All models were simplified by sequential deletion of independent variables and interaction terms from all full models based on Akaike's Information Criterion (AIC, Burnham & Anderson, 1998; Johnson & Omland, 2004) until the minimum adequate models were reached. Residuals were checked using diagnostic plots. We used Moran's I autocorrelation coefficient (Moran, 1950) to proof that there is no spatial autocorrelation of the study sites regarding SR, FD, and PD, respectively their changes.

All analyses were run using the statistical software R 2.9.2 (R Development Core Team, 2009). Packages used for FD calculations include car (Fox, 2008), gtools (Warnes, 2009), cluster (Maechler et al., 2005), and clue (Hornik, 2009). For PD calculations we used packages ape (Paradis et al., 2004) and vegan (Oksanen et al., 2009). Moran's I was also calculated using package ape.

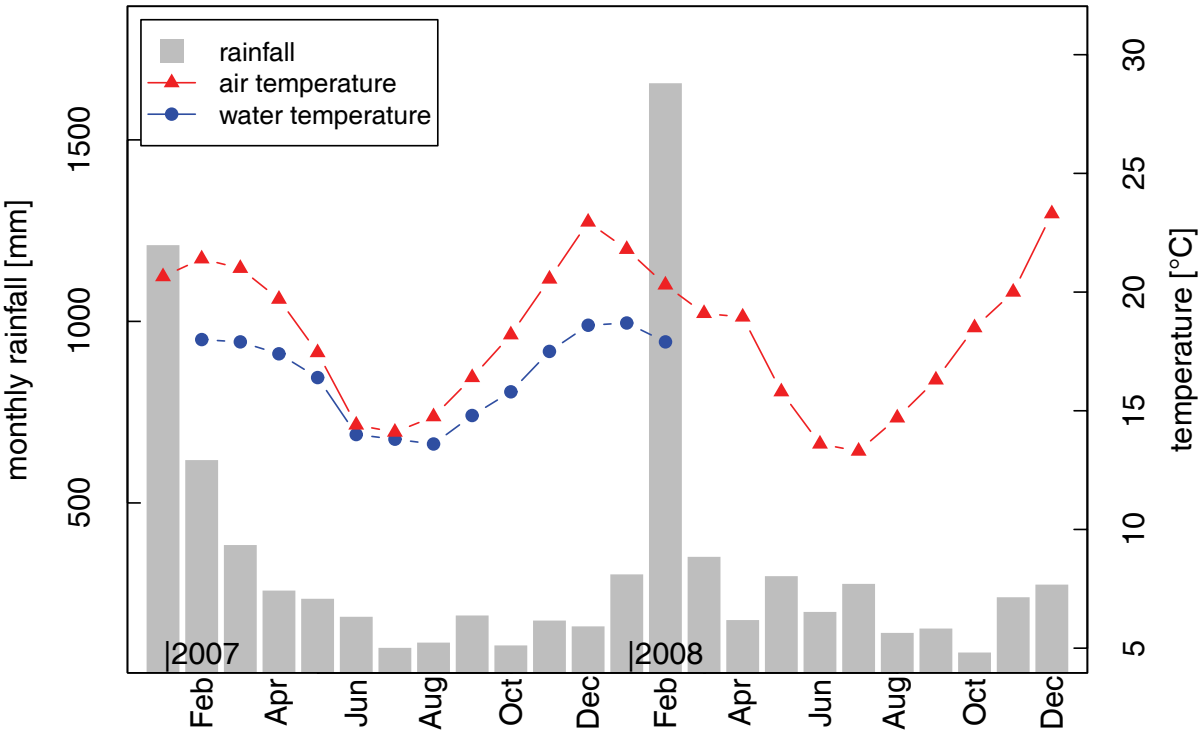


**Figure 1** Annual changes in precipitation and temperature from the RNP region from January 2007 to December 2008. The total monthly precipitation is given in grey bars. The curves represent the mean monthly temperature retrieved from daily minimum-maximum-measurements of air temperature (red triangles) and the stream water temperature (blue circles; data from Fompohonina River). Data of rainfall and air temperature were provided by ValBio research station, water temperature was retrieved from iButton temperature loggers.

## Results

There is no completely dry season in the summer months in RNP, however, in single months the precipitation can fall under 100 mm. The wet season in winter is characterised by high precipitation whereas the maximum can vary between months (see e.g. January 2007 *vs.* January 2008 and February 2007 *vs.* February 2008; Figure 1). Temperature of both, air and water of streams shows pronounced seasonality with higher temperatures during winter/rain season and lower temperatures during summer/dry season (Figure 1).

*Species richness* – Summarizing data over wet and dry seasons, we found tadpoles of a total of 31 species in all twelve stream section (= communities). In the wet season only we found 5 to 15 species, in the dry season 2 to 12 species per community. SR in the dry season was about 27% lower than in the wet season (paired t-test, $t = 3.44$, $df = 11$, $p = 0.006$). Beside this loss in SR,

in 8 streams species turnover from wet to dry season was observed. This means, a community harboured one or more species in the dry season that were not present in the same community during the wet season. However, no species was exclusively found in the dry season.

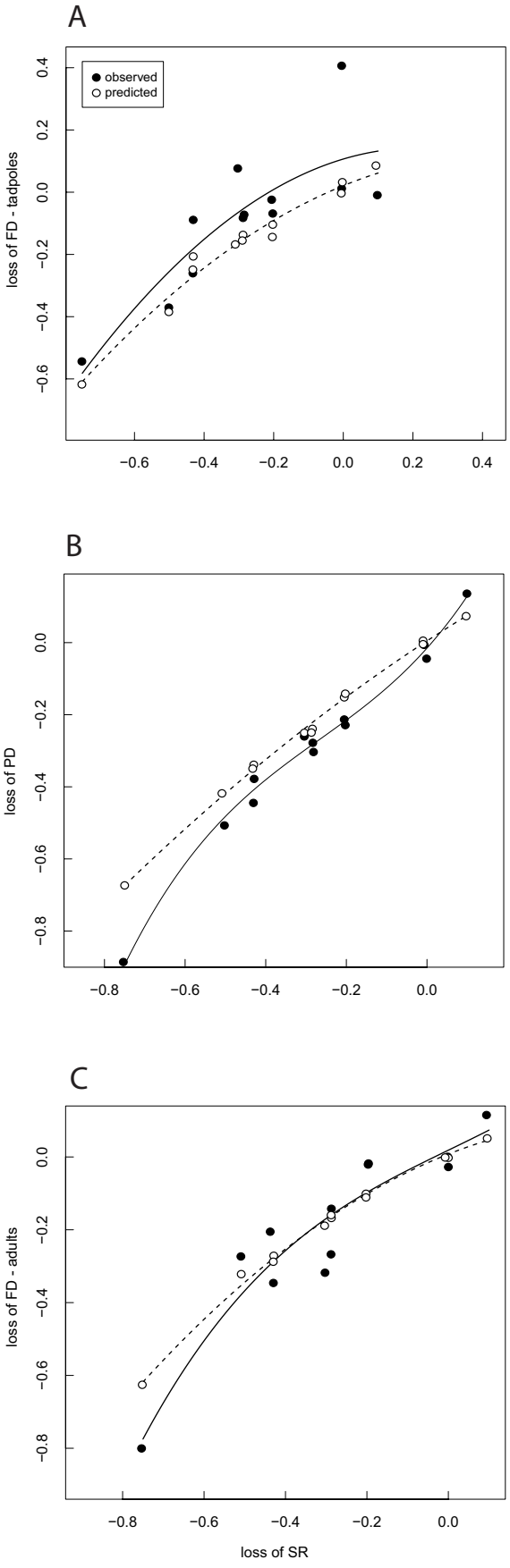


**Figure 2** Loss of (A) FD of tadpoles, (B) PD, and (C) FD using adult traits as function of loss of SR. White circles with black margins show predicted values, the dashed line the respective (polynomial) regression. Black circles show the observed loss in FD, the respective (polynomial) regression is given as solid line.

**Functional diversity**

For null model validation, we tested whether predicted changes in FD of tadpole communities are correlated with the loss of SR and whether this correlation describes a 1:1 relation. We predicted a loss of FD highly correlated with the loss of SR, however, these data describe a curvilinear function (Figure 2; polynomial regression; $R^2 = 0.98$, $F_{2,9} = 179.1$, $p_{model} < 0.001$, $p_{intercept} = 0.37$, $p_{SR} < 0.001$, $p_{SR\hat{}2} = 0.006$). As we have curvilinearity, these predicted values have to be used as null model rather than a 1:1 relation.

As predicted, we observed a loss of FD in the communities that was highly correlated with changes in SR describing a curvilinear function (Figure 2; polynomial regression; $F_{1,10} = 21.3$, $p_{model} < 0.001$, $p_{SR}$ = removed from model (n.s.), $p_{SR\hat{}2} < 0.001$). However, the observed loss of FD differs from the predicted loss of FD (one-sample t-test, $t = 2.32$, $df = 11$, $p = 0.04$; Figure 3). Given the observed loss in SR, we predicted a loss of FD of 17% on average. We observed a loss of FD of only 8%. From this deviation it can be concluded that from the wet to the dry season, species loss and/or species turnover is non random with respect to the species function. The reason for this deviation can be found in the tadpole communities from the dry season: in the wet season, both observed and predicted FD are highly correlated with SR (Figure 4A; linear regressions; predicted: $R^2 = 0.84$, $F_{1,10} = 51.4$, $p_{model} < 0.001$, $p_{intercept} = 0.015$, $p_{SR} < 0.001$; observed: $R^2 = 0.79$, $F_{1,10} = 37.4$, $p_{model} < 0.001$, $p_{intercept} = 0.008$, $p_{SR} < 0.001$). and there is no difference between observed and predicted FD (Figure 4B; one-sample t-test, $t = -1.18$, $df = 11$, $p = 0.26$). In the dry season, the tadpole communities show a quite different pattern. As predicted by the null model, they are characterised by functional redundancy as indicated by curvilinearity (Figure 4C; polynomial regressions; predicted: $R^2 = 0.96$, $F_{2,9} = 104.6$, $p_{model} < 0.001$, $p_{SR} < 0.001$, $p_{SR\hat{}2} < 0.001$, observed: $R^2 = 0.91$, $F_{2,9} = 44.5$, $p_{model} < 0.001$, $p_{SR} = 0.003$, $p_{SR\hat{}2} < 0.03$). Figure 4C shows that these communities show high functional diversity, i.e. observed FD values are higher than predicted (one-sample t-test of deviation; $t = 2.93$, $df = 11$, $p = 0.014$).

Summarising the results concerning FD, we can say that a loss and/ or turnover of species in tadpole communities in RNP from the wet to the dry season is non random with respect to species function. The differences between the seasons are most likely due to patterns of high functional diversity (and functional redundancy) in the dry season, whereas in the wet season FD does not provide more diversity information than SR.

Briefly summarising the results of FD analysis that are based on tadpole community composition but refer to the traits of the respective adults, predicted and observed losses are highly correlated with the loss of SR describing a curvilinear function (predicted: polynomial regression;

$R^2 = 0.998$, $F_{2,9} = 1825$, $p_{model} < 0.001$, $p_{intercept} = 0.14$, $p_{SR} < 0.001$, $p_{SR^2} < 0.001$; observed: polynomial regression; $F_{2,9} = 37.2$, $p_{model} < 0.001$, $p_{SR} = 0.019$, $p_{SR^3} < 0.04$). However, both functions include highly influential data points and the curvilinearity needs to be considered with care. In contrast to the loss of FD based on tadpole traits, the observed loss of FD (adults traits) did not differ from the predicted values (one-sample t-test, $t = -0.45$, $df = 11$, $p = 0.68$, Figure 3). We also found no difference between SR and predicted and observed FD (adult traits) neither in the dry nor in the wet season.

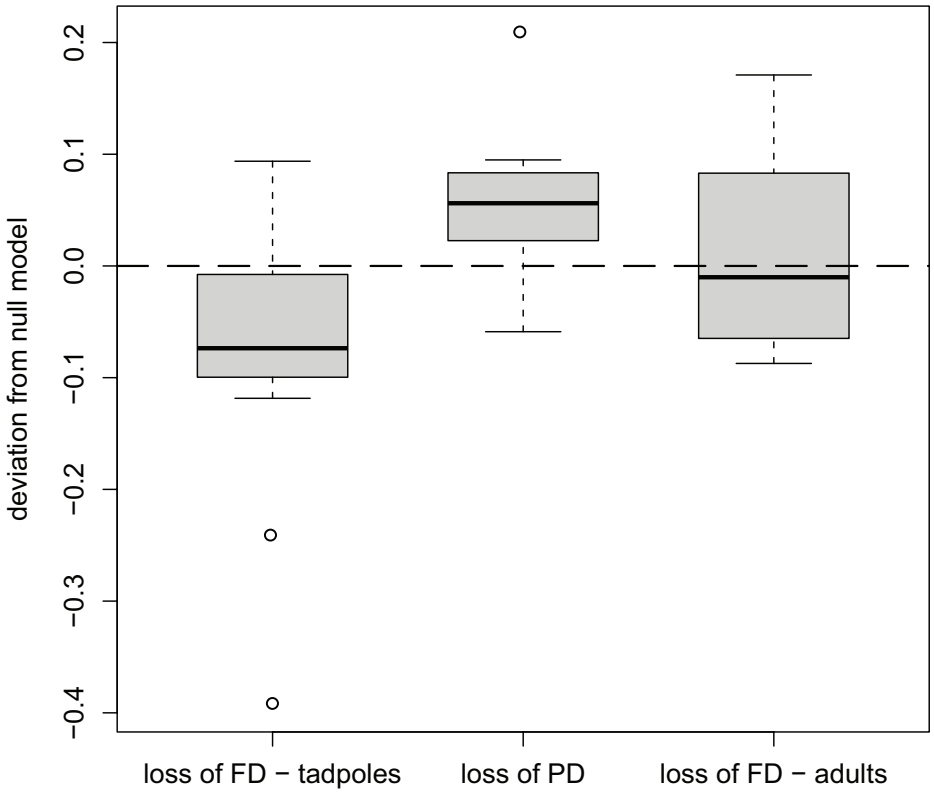


**Figure 3** Deviation of observed loss of FD of tadpoles, PD, and FD of adults from the predicted values (null model). The dashed line represents the null model, the boxes the observed data. Values below the dashed line show less loss, values above the line show a higher loss than predicted. FD of tadpoles decreases significantly less than predicted whereas PD decreases significantly more than predicted. FD calculated using traits of adults did not differ from the null model.

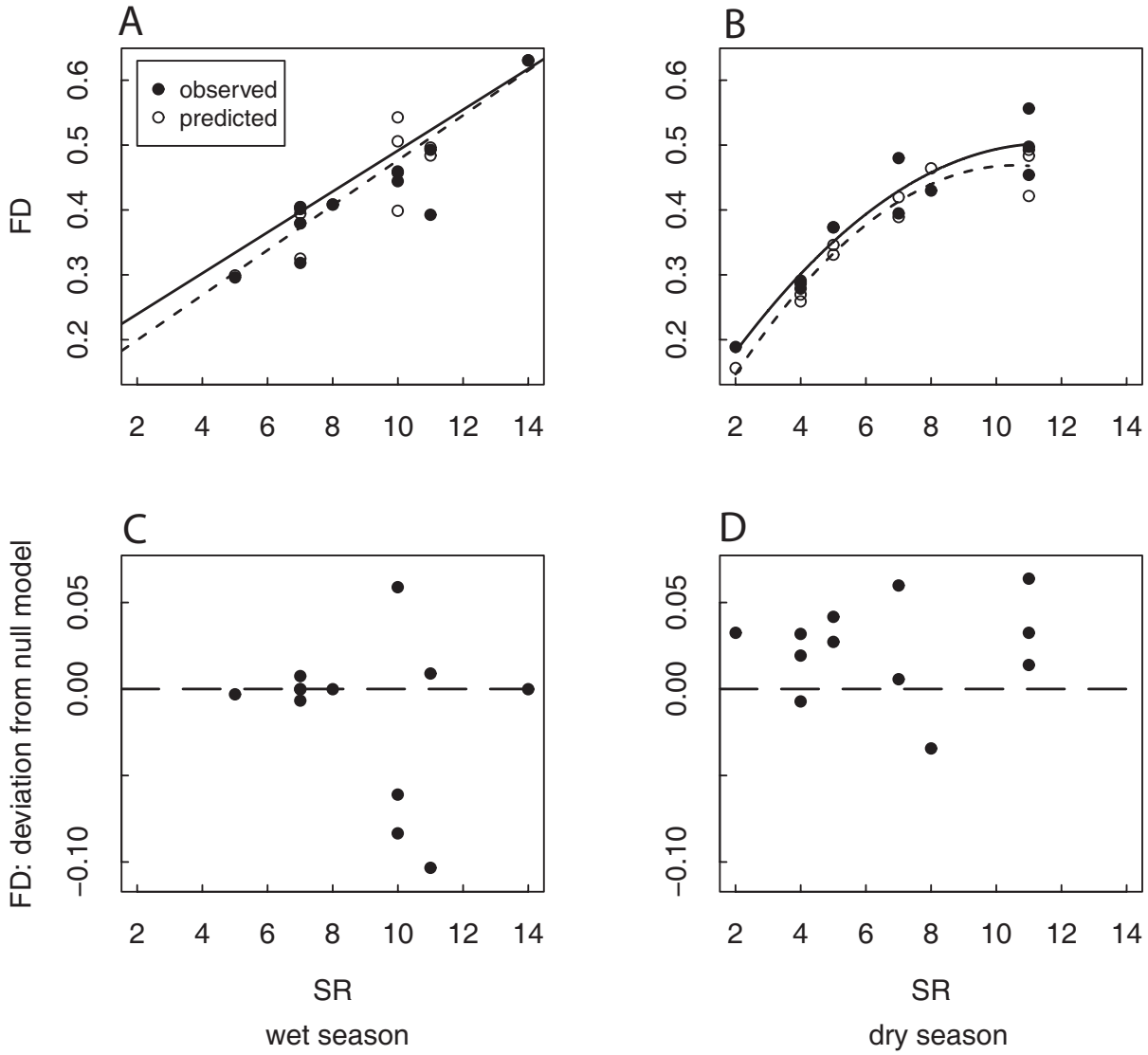


**Figure 4** Comparing predicted and observed FD from tadpole communities from RNP. Given are observed (black filled circles, continuous regression line) and predicted FD (white circles with black margins, dashed line) along a SR gradient for the wet (A) and the dry season (B). (C) and (D) show the differences between null model (predicted data, dashed line) and the observed data of FD of the wet and dry season, respectively. Values above or below the line show observed data being higher (high FD) or lower (low FD) than predicted, respectively. Differences were not significant in the wet season; in the dry season communities show significant high FD.

### Phylogenetic diversity

The null model for loss of PD correlated with the observed loss of SR but differed significantly from a simple 1:1 relation. As for FD, we predicted a loss of PD being highly correlated with the loss of SR describing a curvilinear function (Figure 2B; polynomial regression; $R^2 = 99.9$, $F_{2,9} = 2992$, $p_{model} < 0.001$, $p_{intercept} = 0.63$, $p_{SR} < 0.001$, $p_{SR\hat{}2} < 0.001$). Due to this pattern, predicted values for changes in PD are the preferred null model rather than a 1:1 model.

As for the predicted data, also the observed loss of PD was highly correlated with the loss of SR; by contrast, this correlation describes a cubic polynomial function (Figure 2B; polynomial regression; $R^2 = 0.99$, $F_{3,8} = 377.6$, $p_{intercept} = 0.28$, $p_{SR} < 0.001$, $p_{SR^2} = 0.018$, $p_{SR^3} = 0.006$).
This apparent difference between observed loss of PD and the null model (predicted loss) was significant (one sample t-test; $t = -3.03$, $df = 11$, $p = 0.011$). Given the observed loss in SR, we predicted a loss of PD of 23% but observed a loss of 28%. Therefore, loss of PD was stronger than we predicted by random assembling (Figure 3).

To identify the reason for this deviation of the observed data from the null model, we focused on PD in the wet and the dry season separately. Again, we identified the dry season as main cause. In the wet season, both observed and predicted PD is highly correlated with SR (Figure 5A; linear regressions; predicted: $R^2 = 0.96$, $F_{1,10} = 268.2$, $p_{model} < 0.001$, $p_{intercept} = 0.022$, $p_{SR} < 0.001$; observed: $R^2 = 0.93$, $F_{1,10} = 123.8$, $p_{model} < 0.001$, $p_{intercept} = 0.008$, $p_{SR} < 0.001$). The observed PD of tadpole communities in the wet season does not differ from the predicted values (Figure 5C; one-sample t-test; $t = -0.92$, $df = 11$, $p = 0.38$). Therefore, there is neither phylogenetic redundancy nor phylogenetic clustering or overdispersion in tadpole communities in the wet season. In the dry season, PD of tadpole communities shows a very different pattern. Random communities predict that in the dry season PD will be highly correlated with SR with a non significant trend to curvilinearity (Figure 5B; polynomial regression; $R^2 = 0.99$, $F_{2,9} = 378.2$, $p_{model} < 0.001$, $p_{intercept} = 0.82$, $p_{SR} < 0.001$, $p_{SR^2} = 0.06$). Observed communities do not follow this prediction: their PD is highly correlated with their SR but describing a strong cubic polynomial function (Figure 5B; polynomial regression; $R^2 = 0.99$, $F_{3,8} = 217.5$, $p_{model} < 0.001$, $p_{intercept} = 0.004$, $p_{SR} < 0.001$, $p_{SR^2} = 0.002$, $p_{SR^3} = 0.002$). As indicated in Figure 5D, PD of tadpole communities in the dry season is significantly lower than predicted (one-sample t-test, $t = -3.57$, $df = 11$, $p = 0.004$). Therefore, in the dry season tadpole communities show phylogenetic clustering. They harbour species that are closer related to each other than expected by chance.

Summarising the results concerning PD, species loss and/or turnover from the wet to the dry season is non-random with respect to the degree of relatedness of the species. This non-randomness depends on the level of change in SR and is expressed in phylogenetic clustering in the tadpole communities in the dry season (Figure 2 and Figure 5B, D).

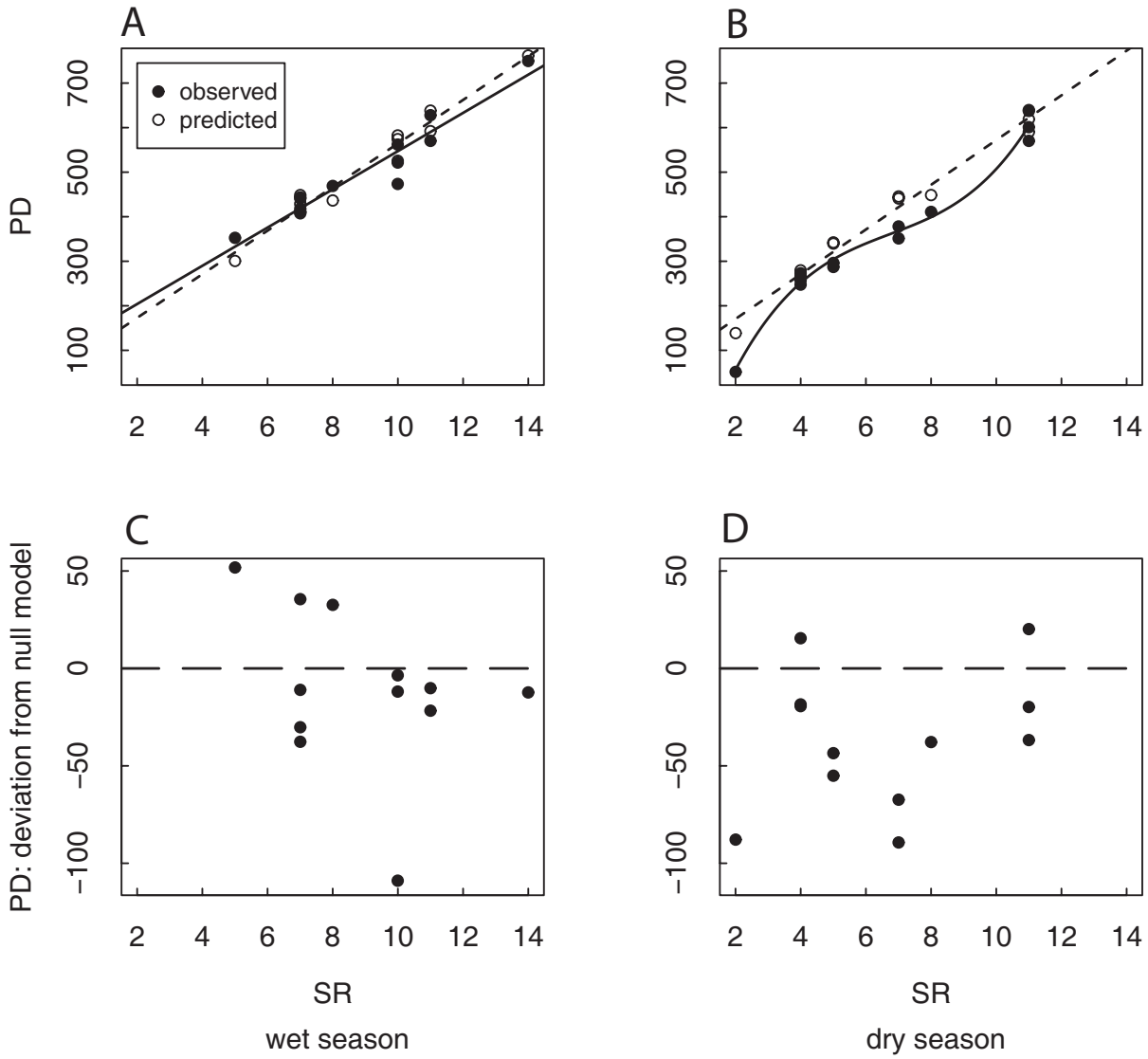


**Figure 5** Comparing predicted and observed PD from tadpole communities from RNP. Given are observed (black filled circles, continuous regression line) and predicted PD (white circles with black margins, dashed line) along a SR gradient for the wet (A) and the dry season (B). (C) and (D) show the differences between null model (predicted data, dashed line) and the observed data of PD of the wet and dry season, respectively. Values above or below the line show observed data being higher (phylogenetic overdispersion) or lower (phylogenetic clustering) than predicted, respectively. Differences were not significant in the wet season; in the dry season communities show significant phylogenetic clustering.

# Discussion

Seasonality as observed in the tropical rainforest of Madagascar causes changes in SR, FD, and PD of tadpole communities. All of these measures of diversity indicate a decreased diversity in the dry season compared to the wet season. However, FD and PD do neither change congruent to SR nor to each other. Furthermore, changes as observed differ significantly from our predictions. This demonstrates that annual climatic changes cause tadpole community composition to change depending on tadpole functional traits and tadpole relatedness. The loss of functional diversity from the wet to the dry season was weaker than predicted. Interestingly, the opposite pattern was the case for PD: it changed stronger than predicted. Whereas in the wet season all three measures provide the same information on tadpole community, strong differences are found in the dry season. During the latter they are characterised by functional redundancy and high functional diversity, but also by phylogenetic clustering.

### Loss of species richness

From the wet to the climatically less suitable, colder dry season (Both et al., 2009) species diversity in tadpole communities decreased significantly. Tropical seasonality has been shown to affect frog activity and tadpole SR at ponds (Kopp & Eterovick, 2006; Both et al., 2009) but not always at streams (Andreone, 1996; Afonso & Eterovick, 2007), indicating often more stable conditions in streams than in ponds (Eterovick & Barata, 2006). Beside loss of SR, communities can change in composition by species turnover (Ernst et al., 2006), and also the observed tadpole communities were characterised by species turnover. This is often due to species that are seasonal specialists (Choi et al., 2010), however, no species in this study can be classified as specialised on a season and breeding takes part throughout the year.

### Loss of functional diversity

As expected due to the observed loss of species diversity from the wet to the dry season, tadpole communities also show a loss of FD (Strauß et al., 2010). Interestingly, the loss of FD is less than predicted, and there is high FD in dry season. Also for tropical beetle communities seasonal loss of species depends on ecological traits (Grimbacher & Stork, 2009). Here it means that only these species remain that show less overlap in morphology and therefore ecological function (Petchey et al., 2007). This is an indication that these communities are shaped by competition

(Petchey et al., 2007). So far, competition was assumed to be not of importance for stream tadpole communities (Inger et al., 1986; Eterovick & Barata, 2006; Strauß et al., 2010). These studies, however, were all conducted during wet seasons and correspond also to our data from the wet season. Evidence of competition in tadpole communities came so far only from temporary ponds (Morin, 1983; Morin & Johnson, 1988; Werner & Glennemeier, 1999; Wells, 2007). As the water level in the streams was constant through the year and tadpole densities where rather low (own unpublished data), strongly reduced food availability, e.g. due to reduced algae growth at the low temperatures, may have caused competition.
Additionally, during the dry season these communities show functional redundancy. This means, as more species occur in a community, as more they overlap in their ecological function. The lack of redundancy during the wet season contradicts to previous studies (Strauß et al., 2010). The probability to identify redundancy depends on SR and range of SR of the observed communities (Halpern & Floeter, 2008; Strauß et al., 2010). Here, the range of SR is considerably lower than in the study of Strauß et al. (2010) and the potential weak redundancy in the wet season is not detectable.

### Loss of phylogenetic diversity

Phylogenetic diversity of stream tadpole communities also decreases with a loss of SR. Contrary to the observed pattern for FD, the loss of PD is stronger than predicted and communities show phylogenetic clustering (Emerson & Gillespie, 2008) in dry season. This means that those species disappear from the communities that are less closely related to the other species. Consequently, only during the dry season members of tadpole communities are closer related to each other than expected. Phylogenetic clustering was also observed in several bacterial (Horner-Devine & Bohannan, 2006), insect (Weiblen et al., 2006) and plant communities (Webb, 2000). In general, taxa that are more closely related tend to show a higher ecological similarity than taxa that are distantly related (Harvey & Pagel, 1991) and they share traits necessary to persist environmental filters (Webb et al., 2002). Clustering is therefore often interpreted as caused by environmental filters (Webb et al., 2002; Horner-Devine & Bohannan, 2006). However, in the here studied communities, relatedness of species is not congruent to species function considering both, tadpole traits and adults traits.

### Functional diversity vs. phylogenetic diversity

The morphological and therefore functional similarity of members of tadpole communities does not reflect their relatedness. This is evident during the dry season, when communities have lower SR, FD, and PD than in the wet season, and tadpoles are closer related but functionally more different. FD and PD of communities may be decoupled from SR, e.g. if community changes include species turnover (Ernst et al., 2006). FD and PD should generally be congruent (for references see above). For Madagascan tadpoles, morphology largely fits phylogeny, but there are also exceptions and homoplasy occurs (Grosjean et al., in press; Randrianiaina et al., unpublished). As these exceptions are randomly distributed between the taxonomic groups included in this study, they may not necessarily have influenced the results. If these differences in change of FD and PD were largely influenced by species turnover, tadpoles were replaced by closely related species that have a different morphology.

One may argue instead, that PD reflects traits of adults rather than those of tadpoles. It is known that seasonality acts on frog activity (Andreone, 1996; Kopp & Eterovick, 2006) and the strength of influence depends on species ecology (Gottsberger & Gruber, 2004). If this would be the case, in RNP adult amphibians may pass an environmental filter whereas their larval stages are facing competition. However, as FD of adult traits changes just as expected and corresponding to SR and not as strong as PD, this is unlikely.

The discrepancy of seasonal changes of FD and PD of tadpole communities indicate that, on the one hand, chosen morphological traits of tadpoles are of ecological relevance, they are affected by environmental changes and influence community composition, at least during the dry season. On the other hand, as PD is differently affected. PD therefore encodes for traits of ecological relevance that have not been covered by morphological traits. PD may be stronger correlated with physiological or behavioural species traits which are more conservative than tadpole morphology. With the given state of knowledge on tadpole behaviour and physiology, this can, however, so far not be tested.

### Conclusions

Two main conclusions can be drawn: (1) communities that persist throughout the year in a seasonal environment may underlie different shaping processes, depending on seasonal conditions. Competition may not play a role in the one season but it can be a driving force in another season. (2) All three measures of diversity used in this study are of ecological importance. As they provide different information, they can complement one another but an interpretation can be difficult.

## Authors' contributions

AS participated in the design of the field study, conducted field work, designed and conducted statistical analyses, and drafted the manuscript. FG largely contributed to the programming in R. RDR conducted fieldwork and conducted most of morphological measurements used for FD analysis. MV designed the morphological and the DNA barcoding part and significantly developed the draft. JG designed the field study, conducted fieldwork, and significantly developed the draft.

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# Appendix

**Table 1** Morphological traits of adult frogs used for calculation of FD. All traits were binary and divided into subtraits, if more than two categories existed.

| Morphological trait | Categories |
|---|---|
| snout-vent length | 20-30 mm // 31-40 mm // >40 mm |
| foot webbing | no webbing or traces // moderate or low webbing // largely or fully webbed |
| hand webbing | absent // rudimentary // present |
| connection of outer metatarsalia | unconnected // connected |
| terminal discs of digits | not expanded // slightly expanded // strongly expanded |
| relative tympanum diameter (males) | TD/SVL < 1.0 // > 1 |
| relative head width | HW/SWL < 0.33 // > 0.33 |
| relative head length | HAL/SVL usually < 0.3 // > 0.3 |
| inner metatarsal tubercle | small // large |
| snout / head in dorsal view | rounded // pointed |
| frenal stripe | absent // present |
| vertebral stripe | always absent // sometimes or always present |
| ground colour | green // brown |
| bright iris colour | absent // present |
| dorsal pattern | uniform // indistinctly marked // distinctly marked |
| dorsolateral colour border | absent // present |
| lateral skin flaps | absent // present |
| dorsal ridges | absent // present |
| supraocular spines | absent // present |
| dorsal skin texture | smooth // shagreened-slightly tubercular // coarsely tubercular |
| preferred habits / habitat | semiaquatic // riparian // semiarboreal // terrestrial indep. from water // arboreal |
| diurnality | predominantly nocturnal // predominantly diurnal |
| aposematic colour | absent // present |

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| 01/2008 – 02/2008 | **Forschungsaufenthalt** in **Madagaskar** |
| 02/2007 – 04/2007 | **Forschungsaufenthalt** in **Madagaskar** |
| 05/2006 – 10/2006 | **Projekte** zu Räuber-Beute-Interaktionen mit Eulen und Trauerschnäppern in **Finnland** |
| 03/2006 | **Feldassistent** Rifcon GmbH |
| 07/2003 – 04/2004 | **Diplomarbeit** ("The effects of reduced red fox abundance on bush rat behaviour") in **Victoria (Australien)** (Feldarbeit) |
| 10/2002 – 03/2003 | **Tutor** zur Grundvorlesung "Allgemeine Ökologie" |

## Weitere universitäre Aktivitäten

| | |
|---|---|
| 06/2004 – 07/2005 | Studentische Hilfskraft (Unis Jena, Halle; UFZ Halle) |
| 10/1998 – 03/2003 | Mitglied folgender Gremien studentischer Selbstverwaltung (überschneidend): Fakultätsrat (4 Semester), Studentenrat (4 Sem.), Fachschaftsrat (9 Sem.), Ausbildungsausschuss (4 Sem.) |

## Außeruniversitäre Berufserfahrung

| | |
|---|---|
| 03/1997 – 04/1998 | Zivildienst in Kinderkrankenhaus Greiz; Pflege |
| 11/1996 – 02/1997 | Angestellter im Gestüt Bretmühle |

## Weitere Fähigkeiten

| | | | | |
|---|---|---|---|---|
| **Sprachen** | **:** | Deutsch | - | Muttersprache |
| | | Englisch | - | sehr gut |
| **IT** | **:** | Linux, MS Windows (± MacOS) | | |
| | | Statistikprogramme (R, SPSS, S-Plus) | | |
| | | Graphikbearbeitung (GIMP, Adobe) | | |
| **Interessen** | **:** | Ausdauerlauf, Radfahren, Wandern | | |
| | | Photographie | | |

## Publikationen

Strauß, A., R.-D. Randrianiaina, M. Vences & J. Glos, submitted. Species distribution and community structure of anuran larvae in rainforest streams of Madagascar. Hydrobiologia.

Randrianiaina, R.-D., A. Strauß, J. Glos, F. Glaw & M. Vences, submitted. Diversity, evolution and reverse taxonomy in the specialized tadpoles of Malagasy river bank frogs of the subgenus *Ochthomantis* (genus *Mantidactylus*). Contributions to Zoology.

Hiobiarilanto-Rasolonjatovo, T., R.-D. Randrianiaina, J. Glos, A. Strauß & M. Vences, in press. Description of ten tadpoles in the genus *Boophis* from Madagascar. Zootaxa.

Grosjean, S., A. Strauß, J. Glos, R.-D. Randrianiaina, A. Ohler & M. Vences, in press. Morphological and ecological uniformity in the funnel-mouthed tadpoles of Malagasy litter frogs, subgenus *Chonomantis*. Zoological Journal of the Linnean Society.

Strauß, A., E. Reeve, R.-D. Randrianiaina, M. Vences & J. Glos, 2010. The world's richest tadpole communities show functional redundancy and low functional diversity: ecological data on Madagascar's stream-dwelling amphibian larvae. BMC Ecology 10: 12.

Randrianiaina, R.-D., L. Raharivololoniaina, C. Preuss, A. Strauß, F. Glaw, M. Teschke, J. Glos, N. Raminosoa & M. Vences, 2009. Descriptions of the tadpoles of seven species of Malagasy treefrogs, genus *Boophis*. Zootaxa 2021: 23–41.

Randrianiaina R.-D., R. Navarro Antúnez, J. Canitz, F. Forth, I. Lemme, B. Rodríguez, H. Rinas, R. Thänert, P. Tröger, N. Westphal, A. Willim, K. C. Wollenberg, A. Strauß & M. Vences, 2009. Vogue or adaptive character? A tadpole's goatee helps to distinguish two cryptic treefrog species of the genus *Boophis*. Herpetology Notes 2: 165–173

Schmidt, H., A. Strauß, F. Glaw, M. Teschke & M. Vences, 2009. Description of tadpoles of five frog species in the subgenus *Brygoomantis* from Madagascar (Mantellidae: *Mantidactylus*). Zootaxa 1988: 48–60.

Schmidt, H., A. Strauß, E. Reeve, A. Letz, A.-K. Ludewig, D. Neb, R. Pluschzick, R.-D. Randrianiaina, D. Reckwell, S. Schröder, A. Wesolowski & M. Vences, 2008. Descriptions of the remarkable tadpoles of three treefrog species, genus *Boophis*, from Madagascar. Herpetology Notes 1: 49–57.

Strauß, A., K. Y. Solmsdorff, R. Pech & J. Jacob, 2008. Rats on the run: removal of alien terrestrial predators affects bus rat behaviour. Behavioural Ecology and Sociobiology 62: 1551–1558.

### Tagungsbeiträge

Strauß, A., 2009. Vondron' ny tsiboboka avy any Madagasikara: Artenreichtum, funktionale und phylogenetische Diversität von tropischen Kaulquappengemeinschaften. Geladener Vortrag im Julius-Kühn Institut – Federal Research Centre for Cultivated Plants; Vertebrate Research, Münster, Deutschland, 24. November 2009 (Vortrag).

Strauß, A., 2009. Funktionale Diversität – funktionale Redundanz: Ein anderer Blick auf die Diversität von Kaulquappengemeinschaften. Ecology & Energetics meeting, Hamburg, Deutschland, 04. April 2009 (Vortrag).

Strauß, A., E. Reeve, R.-D. Randrianiaina, M. Vences & J. Glos, 2009. It's not just the number of species: tadpoles' functional diversity along environmental gradients. 6th International Tropical Zoology Symposium "Tropical Vertebrates in a Changing World", Bonn, Deutschland, 03.-08. Mai 2009 (Vortrag).

Strauß, A., R.-D. Randrianiaina, E. Reeve, M. Teschke, M. Vences & J. Glos, 2008. Tropical tadpole communities: distribution patterns and assembly rules. 101st Annual Meeting of the German Zoological Society, Jena, Deutschland, 19.-22. September 2008 (Vortrag).

Strauß, A., R.-D. Randrianiaina, J. Glos & M. Vences, 2007. Why are there so many species? – Understanding hyperdiverse tropical tadpole communities. 14th European Congress of Herpetology and SEH Ordinary General Meeting, Porto, Portugal, 19.-23. September 2007 (Vortrag).

Strauß, A., K. Y. Solmsdorff & J. Jacob, 2005. Rats on the run? – The effects of red fox abundance and cover on bush rat behaviour. 35th Annual Conference of the Ecological Society of Germany, Switzerland and Austria, Regensburg, Germany, 19.-23. September 2005.

Strauß, A., K. Y. Solmsdorff & J. Jacob, 2005. Behavioural response of bush rats to the management of introduced predators. 5th European Vertebrate Pest Management Conference, Budapest, Hungary, 5-8 September 2005.